THREE-DIMENSIONAL TOMOGRAPHIC RECONSTRUCTION OF AN EXCEPTIONALLY WELL PRESERVED ICHNOLOGICAL ASSEMBLAGE FROM THE STAINMORE FORMATION, CARBONIFEROUS, UK.

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ABSTRACT

This Ph.D. thesis addresses current issues with ichnotaxonomic practice, and characterizes an exceptionally well preserved ichnological assemblage from the Carboniferous Stainmore Formation, Northumberland, United Kingdom. Samples were collected from closely localized float representative of various units throughout the succession, which was deposited in a storm-dominated marine shoreface. Three dominant ichnotaxa were selected for three-dimensional morphological analysis due to their complicated morphology and/or unclear taxonomic status: 1) *Dactyloidites jordii* isp. nov.; 2) *Beaconites capronus*, and; 3) *Neoeione moniliformis* comb. nov. Using serial grinding and photography, these ichnotaxa were ground and modelled in true colour.

High-resolution models of three taxa produced in this study are the basis of the first complete three-dimensional consideration of the traces, and forms the basis for refined palaeobiological and ethological analysis of these taxa. *Dactyloidites jordii* isp. nov. is a stellate to palmate burrow composed of numerous long, narrow rays that exhibit three orders of branching arranged into tiered galleries radiating from a central shaft. It is considered to be the feeding structure produced by a vermiform organism. *Beaconites capronus* is a winding trace with distinctly chevron-shaped, meniscate backfill demonstrated herein to backfill the vertical shafts associated with its burrows in a comparable fashion to the horizontal portion of the burrow. This lack of a surface connection would result in the trace making organism being exposed to low-oxygen porewater. Coping with this porewater dysoxia could be approached by burrowing organisms in a number of ways: 1) revisiting the sediment-water interface; 2) creating periodic shafts; or 3) employing anaerobic metabolism. *Neoeione moniliformis* was originally introduced as *Eione moniliformis,* however, the genus *Eione* Tate, 1859 is a junior homonym of *Eione* Rafinesque, 1814. This led to the transfer of *Eione moniliformis* to *Parataenidium*. Through careful examination and three-dimensional characterization of topotypes, the transfer to *Parataenidium moniliformis* is demonstrated herein to be problematic, as *Parataenidium* refers to primarily horizontal burrows with two distinct layers and *Eione moniliformis* is composed of one distinct level. As such, the new ichnogenus *Neoeione* is created to accommodate *Neoeione moniliformis*.

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CO-AUTHORSHIP STATEMENT

This doctoral dissertation is composed of five chapters. Chapters two through four are prepared in manuscript format, each of which has been submitted to an international scientific journal as indicated on the chapter title page. Chapter one is an introductory chapter that provides a review of the pertinent literature, guidelines to the practice of ichnotaxonomy, and a review of the geological and ichnological study area to contextualize the content of chapters two through four. I am the sole author of chapter one and have written the entirety of its content, receiving only editorial assistance. Chapters two through four were a collaborative effort between myself, as primary author, and Dr. Duncan McIlroy, co-author.

Chapter 2 – Boyd and McIlroy, submitted to *Geobios*

The field location and target samples were specified by Dr. McIlroy prior to any field work being completed. Sample collection and field logging was completed by myself, with the assistance of Dr. Michael Garton. Upon returning to Memorial University I completed the sample preparation and processing. XRD analysis was completed with the assistance of Edgars Rudzitis. As the lead author, I was primarily responsible for the data analysis and interpretation; Dr. McIlroy provided editorial and supervisory assistance along with his expertise in ichnology.

Chapter 3 – Boyd and McIlroy, submitted to *Ichnos*

The field location was specified by Dr. McIlroy. I collected the samples with the assistance of Dr. Garton. I selected the ichnotaxon to be processed and completed the sample preparation and processing, as well as the data analysis and interpretation. Dr.

McIlroy provided editorial and supervisory assistance along with his expertise in ichnology.

Chapter 4 – Boyd and McIlroy, submitted to *Journal of Paleontology*

The field location was chosen by Dr. McIlroy, and the field work and sample collection was completed by Dr. Garton and me. After selecting the ichnotaxon to be studied, I completed the sample preparation and processing. I analysed and interpreted the data, as well as prepared the manuscript with editorial and supervisory assistance provided by Dr. McIlroy.

Chapter 5 – Boyd and McIlroy, Prepared for submission to the *Proceedings of the Yorkshire Geological Society*

This chapter provides a systematic summary of the ichnological assemblage in the study area, which was selected by Dr. McIlroy. Field work was aided by Dr. Garton. Field photographs were taken by Dr. McIlroy and me. I prepared the manuscript with editorial and supervisory assistance provided by Dr. McIlroy.

Chapter 6 – provides a summary of the included manuscripts in the context of the current understanding of ichnotaxonomy and the objectives set out for this dissertation, as outlined in Chapter 1. I am the sole author of this chapter, having only received editorial assistance.

In addition to the six chapters presented herein an additional paper can be found as Appendix A. This paper was a collaborative effort of all six co-authors involved. As a co-author I helped develop the modelling techniques, in particular with respect to the precise photography of the samples and processing of the images. As such I, along with Dr. Liam

Herringshaw prepared the first draft of the photography subsection and assisted with other elements of the manuscript. Additionally I assisted with editing the manuscript.

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CHAPTER ONE

1. Introduction to ichnology and literature review

Ichnology, or the indirect study of organisms via the traces they leave (*e.g.* tracks, burrows and faeces), is common in nature in the form of tracking prey, and as such has been practiced since early humans. The formal scientific study of ichnology is a relatively new field, with the first published mention of ichnology occurring in 1858 (Hitchcock, 1858). The field of ichnology is subdivided into palaeoichnology (the study of fossilized tracks and traces) and neoichnology (the study of modern traces).

The study of applied ichnology is a blend of both geology and palaeontology, and can be of benefit to both fields of study (McIlroy, 2008). By assessing the ichnological assemblage within a rock unit and delimiting the behaviours involved in modifying the substrate, inferences can be made regarding the palaeoenvironmental conditions during their formation. As ichnology develops it is gaining more acceptance as a critical component of reservoir characterization by petroleum geologists (*cf.* Ekdale *et al.*, 1984; Pemberton *et al.*, 2001; McIlroy, 2004). Organisms are capable of greatly altering the potential reservoir quality of the sediment they inhabit and act upon; this emphasizes the need to characterize the ichnological assemblage and its effect on the sediment (*cf.* Gingras *et al.*, 1999, 2004; Pemberton and Gingras, 2005; McIlroy, 2008; Bednarz and McIlroy, 2009). Ichnology is also being successfully applied to biostratigraphy and the identification of key sequence stratigraphic surfaces (*e.g.* MacEachern *et al.*, 1990; Taylor

and Gawthorpe, 1992; Taylor and Goldring, 1993; Savrda *et al.*, 2001; Taylor *et al.*, 2003; MacEachern and Burton, 2005).

Although ichnological analysis can be used for biostratigraphy and palaeoenvironmental analysis in association with traditional palaeontology methods (*i.e.* macrofossils and microfossils), ichnological analysis has some distinct advantages. As trace fossils are created within the sediment they are fossilized in, sedimentary reworking is not an issue; unlike certain body fossils (Seilacher, 1967). Since a single trace maker can produce a multitude of traces through its lifetime, and multiple types of organisms can produce the same kind of trace, trace fossils are both abundant and pervasive throughout the sedimentological record and across long time ranges. The practical application of ichnology is, however, dependant up the proper identification and differentiation of ichnotaxa using names that convey the maximum amount of information in a clear and efficient manner.

1.1 History of ichnology

Neoichnology has been practiced since the Palaeolithic times (as documented in Australian aboriginal art), however the study of palaeoichnology remained unknown until much later in history (Baucon *et al.*, 2012). The Renaissance period led to a greater understanding and a more scientific approach to ichnology (Baucon *et al.*, 2012). The work done throughout this time however was not carried forward from one scientist to another resulting in largely disjointed studies (Baucon *et al.*, 2012). Notable work from this era in ichnology includes draftings and palaeoenvironmental inferences based on

marine vermiform traces by Leonardo da Vinci *c.* 1500, the "founding father of ichnology" (Baucon, 2010; Baucon *et al.*, 2012).

The study of ichnology remained discontinuous until the 1800's, when various trace fossils were incorrectly considered as the fossilized remains of plants. In 1823, botanist Adolphe Brongniart (1823) published his paper, *"Observations sur les* Fucoïdes *et sur quelques autres plantes marines fossiles"* (Osgood, 1970, 1975). Brongniart used the genus Fucoides to describe fossils from the Italian Alps that he compared to the modern brown algae, *Fucus* (Baucon *et al.*, 2012). The idea of a botanical origin for trace fossils was not unique to Brongniart (*cf.* von Schlotheim, 1822), however due to his prominence in the scientific community, Brongniart's ideas, and the term 'fucoid', became widely accepted (Baucon *et al.*, 2012). As a result, numerous modern ichnotaxa were first misidentified as fucoids (*e.g.*, *Rhizocorallium*, *Scolicia*, *Daedalus*, *Paleodictyon*, *Spirophyton*, *Diplocraterion*, and *Zoophycos;* Osgood, 1970).

The concept of a botanical origin for trace fossils remained prevalent despite published work demonstrating an ichnological origin, linking modern tracemaking activity to fossilized traces (*e.g.* Salter, 1857; Hancock, 1858; Nathorst, 1881), until *c.* 1925 (Osgood 1975; Baucon *et al.*, 2012). Interest in ichnology declined following the understanding that trace fossils lacked a botanical origin, likely influenced by both questionable application of 'fucoids' as biostratigraphic indicators of shallow marine settings and the taxonomic uncertainty in naming trace fossils (Osgood, 1975; Baucon *et al.*, 2012). Despite this, significant progress was made at the Senckenberg Laboratory through the application of uniformitarianism to the study of modern traces from the North Sea to gain insight into fossilized traces (Richter, 1927; Cadée and Goldring, 2007).

It was, however, the advent and application of the 'ichnofacies' concept in 1953 by Adolf Seilacher that highlighted ichnology as a useful tool for inferring palaeoenvironmental conditions. The ichnofacies methodology involves making inferences of the palaeoenvironmental conditions at the time of deposition on the basis of the specific ichnological assemblage present (Seilacher, 1967). This classification facilitated inferences on palaeoenvironmental conditions such as salinity, oxygen levels, nutrient levels, and, perhaps most importantly, environmental energy. Prior to the ichnofacies concept, trace fossils were described and classified in a similar fashion to body fossils (Seilacher, 1953). The development of the ichnofacies concept replaced this methodology with one of an ethological or preservational basis. Following the work of Adolf Seilacher in the 1950's, and given its potential applications, a renewed focus on ichnology has occurred (Seilacher, 1953; Baucon *et al.*, 2012).

In the decades following the advent of the ichnofacies method, the study of ichnology has developed into a much more objective study used in direct association with palaeontological and sedimentological data (McIlroy, 2008). When used in combination, ichnological analysis is a useful tool for facies characterization (McIlroy, 2008). This is particularly the case when sediment incorporated into the burrow fill represents a depositional event that is later winnowed or eroded away, facilitating the preservation of sedimentological data that would otherwise be lost (cf. Wetzel, 2015).

1.2 Introduction to ichnotaxonomy

The goals for the taxonomy of ichnotaxa are ultimately the same as those for biotaxa; to identify, describe, name, and classify various taxa (Goldring *et al.*, 1997). Trace fossils can provide a diverse wealth of information (*e.g.* evolutionary, palaeoecological, stratigraphic, palaeoenvironmental, etc.) and as such, proper ichnotaxonomy is essential to effectively convey the greatest amount of information (Seilacher, 1953; Bromley, 1996; Goldring *et al.*, 1997; McIlroy, 2008; Wetzel, 2015). This is problematic due to five reasons: 1) Many ichnotaxa where originally introduced as fossilized plants or animals (*cf.* Nathorst, 1881; Osgood 1975; McIlroy, 2004; Baucon *et al.*, 2012); 2) Type material for many older ichnotaxa was never collected or has subsequently been lost or destroyed (Pemberton and Frey, 1982); 3) The recent proliferation of ichnogenera, with more valid ichnogenera having been erected after 1987 than have ever been erected prior to that date (Knaust, 2012); 4) Many early ichnotaxa have been deemed *nomina nuda*, *nomina dubia*, or *nomina oblita* (Häntzschel and Kraus, 1972; Bromley and Fürsich, 1980; Rindsberg, 2012); 5) Inconsistent coverage and application of a governing set of guidelines (*cf.* ICZN, 1961, 1964, 1985, 1999; McIlroy, 2004).

Taxonomy is regulated and governed internationally based on the specific branch of life being addressed. The taxonomy of bacteria is governed by the International Code of Nomenclature of Bacteria (ICNB); algae, fungi, and plant taxonomy is regulated by the International Code of Nomenclature for Algae, Fungi, and Plants (ICN; formerly the International Code of Botanical Nomenclature, ICBN); and zoological taxonomy is governed by the International Code of Zoological Nomenclature (ICZN). As there is no

dedicated code for the taxonomy of trace fossils, and trace fossils can be made by plants, animals, and microbes alike, a potential jurisdictional issue arises when the trace maker cannot be confidently assigned. Of the existing codes only the ICZN has given any recognition to trace fossils, which has, unfortunately, not been consistent or straightforward from one edition to the next (*cf.* ICZN, 1961; 1964; 1985; 1999).

1.3 History of ichnotaxonomy

Towards the end of the nineteenth century it became obvious that in order for taxonomy to progress as a consistent and effective science it required international consensus and governance. Thus the International Congress of Zoology was created in 1895 (ICZN, 1961). The congress officially adopted a pre-existing French nomenclatural guide in 1901, and "Règles Internationales de la Nomenclature Zoologique" was translated to English and German and published in 1905; these "rules" were the first universally accepted zoological nomenclature code (ICZN, 1961).

In the early days of formal ichnology trace fossils were typically unrecognised and, as such, named as body fossils (Nathorst, 1881; McIlroy, 2004; Rindsberg, 2012). In some instances specimens were correctly identified as trace fossils and the maker of such traces were unknown, in these cases the trace was used in proxy for the unknown organism which could be named on the basis of the trace alone (Rindsberg, 2012).

When an over-zealous entomologist apparently began naming species of wasps based on plant galls thought to be produced by an unknown gall wasp (cf. Rindsberg, 2012), the ICZN (1961) reacted by banning any of the works of animals that were not accompanied by a known maker (ICZN, 1961; Rindsberg, 2012). This was incorporated

into the first edition of the ICZN (1961). This ruling invalidated all ichnotaxa that could not be assigned a given tracemaker after the cut-off date of December 31, 1930 (ICZN, 1961; Pickerill, 1994; McIlroy, 2004; Rindsberg, 2012). This ruling provided a challenge for individuals working in ichnotaxonomy whereby many trace fossil names entered taxonomic limbo and could only be used in the vernacular (Pickerill, 1994). The majority of confusion that could have resulted was largely avoided as ichnologists persuaded workers to continue practicing ichnotaxonomy as if they had the support of the ICZN, and petitioned for amendments (Bromley and Fürsich, 1980; Pickerill, 1994; McIlroy, 2004; Rindsberg, 2012). During this time, Walter Häntzschel compiled Part W of the Treatise on Invertebrate Palaeontology, which synonymized many of the previously misidentified trace fossils (Häntzschel, 1962, 1965, 1975). This work greatly advanced the field of ichnology by consulting essentially everything known about invertebrate trace fossils at that time, thus providing a thorough basis for the progress of ichnotaxonomy (Häntzschel, 1962, 1965, 1975; Pickerill, 1994; McIlroy, 2004).

In 1985 the third edition of the ICZN was published, in which a provision was made that again allowed the naming of trace fossils (ICZN, 1985).

> "Article 1, a) - Zoological nomenclature is the system of scientific names applied to taxonomic units (taxa; singular: taxon) … names based on the fossilized work of animals (ichnotaxa), and names proposed before 1931 based on the work of extant animals." –ICZN, 1985

1.4 International Code of Zoological Nomenclature

Ichnotaxonomy is currently regulated and governed by the fourth edition of the ICZN (1999) which provides a level of stability and management for the naming and classifying of trace fossils beyond the capabilities of the ichnotaxonomic community alone. The ICZN is managed by the International Commission for Zoological Nomenclature, which is a longstanding, well established organization. The commission operates with plenary power allowing it to regulate, moderate, and otherwise overrule the Code in order to maintain nomenclature stability (ICZN, 1999 Arts. 78.1 and 81). As the ICZN only governs zoological nomenclature (and neither the ICN nor the ICNB recognize ichnotaxa), trace fossils with known non-animal producers are not given official scientific names (Tubbs 2003; Rindsberg, 2012). The reality for the vast majority of practicing ichnologists is one of uncertainty with respect to the trace maker (Bertling *et al.*, 2003, 2004; Rindsberg, 2012). This fact has been acknowledged by the Commission by changing the terminology of article one from "fossilized work of animals (ichnotaxa)" (ICZN, 1985, Art. 1a) to "fossilized work of organisms (ichnotaxa)" (ICZN, 1999, Art. 1.2.1). This change in wording has allowed the naming of numerous ichnotaxa with uncertain creators to be included within the code (Bertling *et al.*, 2004).

1.4.1 Scope and exclusions

The ICZN (1999) defines zoological nomenclature as "the system of scientific names applied to taxonomic units (taxa; singular: taxon) of extant or extinct animals" (ICZN, 1999, Art. 1.1). Article 1.2.1 defines the scope of application of the code as:

> "The scientific names of extant or extinct animals include names based on domesticated animals, names based on fossils that are substitutions (replacements, impressions, moulds and casts) for the actual remains of animals, names based on the fossilized work of organisms (ichnotaxa), and names established for collective groups … as well as names proposed before 1931 based on the work of extant animals." – (ICZN, 1999).

Of the seven exclusions to the scope of the code, article 1.3.6 excludes the work of extant animals described after 1930 (ICZN, 1999). Any material based on the work of extant animals which has been assigned after 1930 does not qualify for eligibility as type material (ICZN, 1999; Art 72.5.1). The code regulates the naming of ichnotaxa at the family-group, the genus-group and the species-group rank, with typification (*cf.* ICZN, 1999, Art. 61) being required at the genus and species rank for ichnotaxa named after 1999 (ICZN, 1999; Art 13.3.3, 42.2.1, 42.3.2).

1.4.2 Concerns

Great strides have been made in ichnotaxonomy and nomenclature since the first edition of the ICZN (1961), however there are still concerns that several ichnotaxonomists argue should be addressed in subsequent editions of the code (Bertling *et al.*, 2003, 2004, 2006; Genise *et al.*, 2004, McIlroy, 2004; Nielson and Nielson, 2001; Rindsberg, 2012). Although it is obvious why the zoological code would only apply to animals, and by extension the works of animals, some authors have suggested loosening the phrasing of the code to make an exception for trace fossils of non-animal origin (Bertling *et al.*, 2003, 2004). Although petitioning the ICN and ICNB for coverage is

possible, it would be a time-consuming and lengthy process with no guarantee of success. Also, in the interest of efficiency, it is desirable to keep pertinent regulations for taxonomy together in one code. This is especially the case for ichnotaxonomy, as it is often impractical to delimit the trace producer. This is partly due to multiple organisms being capable of producing the same type of trace, or a single organism being capable of producing multiple traces; for this reason information pertaining to the producer cannot be used to assign taxonomic status (Bromley, 1996; Bertling *et al.*, 2006; Knaust, 2012). The argument for future editions of the ICZN to change the wording of "fossilized works of an animal" to "trace fossil" (as suggested by Bertling *et al.*, 2003, 2004; Genise *et al.*, 2004) in order for ichnologists to have proper protection of trace fossil names, may in fact add additional challenges in addressing the semantics of what qualifies as a "trace fossil".

Article 1.2 (ICZN 1999) defines the scope of the ICZN which restricts ichnotaxa to fossilized material (ICZN, 1999). This has led some authors to question the fossilization point for trace fossils, which is often arbitrarily defined (Nielsen and Nielsen, 2001; Bertling *et al.*, 2006). Three guidelines for the fossilization point of a trace suggested by Bertling *et al.* (2006) are, "'found in lithified sediment'; 'found in pre-Holocene strata'; or 'found below the taphonomically active zone'" (Bertling *et al.*, 2006). Although these guidelines provide an advantageous starting place for workers, specific criteria for the fossilization point are best left to the judgement of the individual worker. A concern however would be the bioturbation of older sediments by modern organisms (Bertling *et al.*, 2006). This is particularly the case for hard-substrate borings (Bertling *et al.*, 2006). Given the fact that delimiting Neocene borings from Holocene

borings is especially difficult, many modern borings that could be named by their maker would be taxonomically ambiguous should they be named as ichnotaxa; naming any modern borings as ichnotaxa is inadvisable (Bertling *et al.*, 2006; Glaub, 2004).

Naming exclusively fossilized material as ichnotaxa is seen by some authors as a measure to ensure that only preservable material is named (Bertling *et al.*, 2006). This measure protects against naming of labile material such as vehicle tire tracks, human urination traces, and structures created by birds as they begin to fly, all of which were named by Reineck and Fleming (1997) and have subsequently been deemed as *nomina nuda* (Bertling *et al.*, 2006). Individuals working with modern traces (neoichnology) and comparative ichnology however would benefit from the ability to name or modify existing names from data observed in the field or laboratory (McIlroy, 2004). This would allow a worker to directly observe behaviours that give rise to structures, in order to lend perspective to the fossil examples. A growing body of neoichnological literature has provided great insight into trace maker activity leading to morphologically recurrent structures (*e.g.* Herringshaw *et al.*, 2010, 2013; Dashtgard and Gingras, 2012). The term "incipient" has been proposed to differentiate modern traces that are compared to fossilized material rather than use modern material for the basis of new taxa (Bromley and Fürsich, 1980).

Several authors have also expressed concern over the phraseology and application of the principle of priority (ICZN, 1999, Art. 23) with respect to ichnotaxonomy, in particular concerning the application to synonymy (Bertling *et al.*, 2006). Article 23.3.2 of the ICZN (1999) states that when any part is named before the whole, or any stage,

generation, form, or sex of a species is named as a distinct taxon, they require synonymization. Organisms often make, re-work, or otherwise change the traces they produce based on their situational needs thus forming a compound trace (*i.e.* a trace which intergrades between multiple distinct components; Figure 1). Considering that no comparative analogue exisits with respect to biotaxa, and synonymization of these distinct traces would be disruptive to practicing ichnologists, Bertling *et al.* (2006) advocated disregarding this principle for compound traces. Disregarding this principle is however unnecessary, in particular as article 23.2 clearly states that "the Principle of Priority is to be used to promote stability and it is not intended to be used to upset a long-accepted name…" (ICZN, 1999). Since an ichnotaxon is defined by the ICZN as "a taxon based on the fossilized work of an organism…" (ICZN, 1999) distinct components of a compound trace, (*i.e.*, those that occur independent of the whole), could be considered as distinct works of the organism and thus do not require synonymization. As no direct comparison can be made between ichnotaxa and biotaxa, decisions regarding synonymization of traces based on well preserved compound taxa should remain at the discretion of the individual worker. Confusion surrounding the differentiation/synonymization of various ichnotaxa could be helped in large part by ichnotaxonomists using a type series rather than a single holotype when introducing new ichnotaxa to capture any inherent variations in morphology.

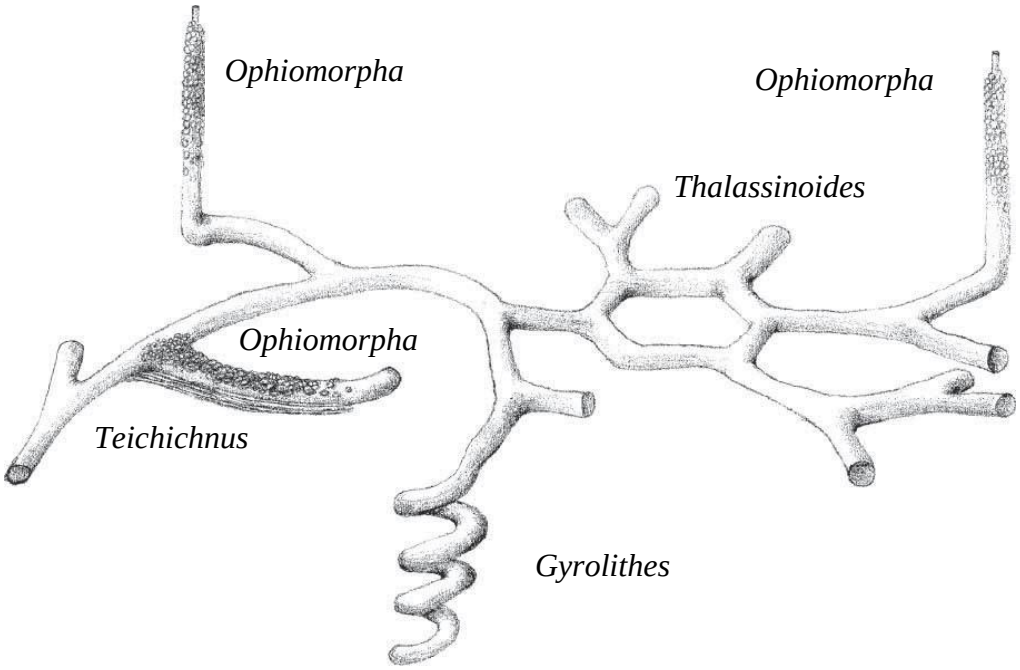

Figure 1. An illustration of a hypothetical compound trace with components of *Ophiomorpha*, *Thalassinoides*, *Gyrolithes*, and *Teichichnus*. (From Bertling *et al.* 2006).

1.5 Ichnotaxa as compared with biotaxa

Taxonomy involves the determination of specific, meaningful criteria (taxobases) for assigning names to organisms and establishing these organisms into groups that are then assigned a rank within a taxonomic hierarchy. For biotaxa, that hierarchy is primarily established on the basis of common ancestry (genetic relationships when determinable), and runs from its highest rank of domain, through kingdom, phylum, class, order, family, genus, to the most contentious rank of species. Of these, species, genus, and family group levels are governed by the ICZN (ICZN, 1999). Sub-units of these taxonomic ranks are also available, albeit not often utilized for ichnotaxa.

The differences between the taxonomy associated with ichnotaxa as opposed to biotaxa are notable; they chiefly regard the establishment and classification of ichnotaxonomic hierarchies. Hierarchies developed for biotaxa tend to be along evolutionary lines; all species within a particular genus are considered to be of closer descent than they are to any species of other genera. This line of reasoning does not apply to ichnotaxa as, unlike biotaxa, different groups of ichnotaxa have no genetic relationships with one another. Any potential genetic relationships existing between the various trace makers are either indeterminable or irrelevant. Considering numerous non-related organisms are known to engage in similar behaviours creating the same traces, evolutionary schemes of organization are impractical (*contra* Ekdale and Lamond, 2003). Furthermore, this lack of a definitive trace-maker for most ichnotaxa rules out genetics as an ichnotaxobase. Although there have been numerous ichnotaxa erected based upon an inferred trace-maker (*e.g. Arenicolites* after the arenicolid polychaetes; Salter, 1857) this practice is discouraged though it does not render a taxon invalid (Bertling *et al.*, 2006; Bertling, 2007).

The taxonomic rank of species is an integral part of the hierarchical system, yet for both ichnotaxa and biotaxa defining this rank is a problematic issue. The species problem for biotaxa results from inconsistencies and confusion regarding the definition of the term "species" itself. There are multiple current and competing definitions/concepts regarding what exactly constitutes a species (Table 1; for a summary see Queiroz, 2007). Considering this, the delimitation of species can be a contentious task (Queiroz, 2007). Although there are multiple definitions of this term (Table 1), all of these definitions

share the concept that distinct species arrive through the evolution of distinct metapopulation lineages (Queiroz, 2007). The problem for ichnotaxonomy with regards to the species group (ichnospecies) is that the differentiation between what qualifies as an ichnogenus versus an ichnospecies is at the discretion of the individual worker (Pickerill, 1994). Although attempts towards empiricism have been made (Bromley, 1990, 1996; Fürsich, 1974 a, b; Goldring *et al.*, 1997), there remains no universally accepted, objective method (Bertling *et al.*, 2006).

As different groups of ichnotaxa have no genetic relationships with one another, establishing ichnotaxonomic classification based solely on the rules of biological classification is fraught with pitfalls. It is therefore important that both the morphology of the structure and the ethology of the trace-making organism are taken into account when considering their classification (Bertling, 2007). Different groups of ichnologists have diverse opinions on which of these characteristics holds more value as ichnotaxobases (Goldring *et al.*, 1997; Ekdale and Lamond, 2003; Bertling *et al.*, 2006; Bertling, 2007; Knaust, 2012). An ethological classification would maximize the use of trace fossils in palaeoenvironmental analyses (Ekdale and Lamond, 2003; Bertling *et al.*, 2006; Bertling, 2007; Knaust, 2012), however this approach is subjective by nature, as the trace-maker itself is often unknown and its ethology cannot confidently be interpreted (Goldring *et al.*, 1997). Alternatively, a classification scheme based primarily on morphology would be much more objective (Goldring *et al.*, 1997), although this method would arguably detract from the usefulness of trace fossils in such studies (Schlirf and Uchman, 2005; Buatois and Mángano, 2011). Many ichnologists agree that it is best to use a combination

of both by describing morphology that is significant with respect to the trace-maker's ethology (Bertling *et al.*, 2006; Bertling, 2007; Knaust, 2012).

Concept	**Property**	**Supporters**
Biological (Isolation/Recognition)	Interbreeding, ability to recognize potential mate	Wright (1940); Mayr (1942); Dobzhansky (1950); Dobzhansky (1970); Paterson (1985); Masters *et al.* (1987); Lambert and Spencer (1995)
Ecological	Occupy the same niche or adaptive zone	Van Valen (1976); Andersson (1990)
Evolutionary	An exclusive evolutionary role	Simpson (1951); Wiley (1978); Mayden (1997); Grismer (1999, 2001)
Cohesion	Genetic or demographic exchangeability	Templeton (1989, 1998)
Phylogenetic (Hennigian, monophyletic, genealogical, diagnosable)	An irreducible group whoses members share a common ancestor	Hennig (1966); Ridley (1989); Meier and Willmann (2000); Rosen (1979); Donoghue (1985); Mishler (1985); Baum and Shaw (1995); Avise and Ball (1990); Nelson and Platnick (1981); Cracraft (1983); Nixon and Wheeler (1990)
Phenetic	Morphologic similarities	Michener (1970); Sokal and Crovello (1970); Sneath and Sokal (1973)
Genotypic cluster	Form a genotypic cluster with few/no intermediates	Mallet (1995)

Table 1. Major contemporary species concepts and their key differentiating properties (Modified from Queiroz, 2007).

1.6 Description/characterization methods

What qualifies as a "trace fossil" is still being debated (Mikuláš, 1999; Bertling *et al.*, 2003, 2004; Tubbs, 2003; Genise *et al.*, 2004; Rindsberg, 2012). According to the ICZN (1999) the term "trace fossil" is synonymous with the "fossilized work of an organism" and can be named under the provisions of the code (ICZN, 1999; Tubbs, 2003). Amendments proposed to the Code suggest replacing the "obsolete term" work of an organism with trace fossil, as there are numerous works of animals that are generally not accepted as trace fossils for the purpose of formal nomenclature, notably soils, embedment structures, pearls, and un-modified secretions, among others (Bertling *et al.*, 2003, 2004; Genise *et al.*, 2004; Bertling *et al.*, 2006, Rindsberg, 2012).

The term trace fossil was introduced by Scott Simpson in 1956 and later defined as "a sedimentary structure resulting from the activity of an animal moving on or in the sediment at its time of accumulation; includes tracks, burrows, feeding and other traces" (Simpson, 1956; Sarjeant and Kennedy, 1973). This definition was later shortened to "indication of the activity of a living plant or animal, preserved in rock or sediment, or in a body fossil" and included stromatolites within this definition (Sarjeant and Kennedy, 1973). This definition again changed to "a morphologically recurrent structure resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate" (Bertling *et al.*, 2006). This definition has been accepted by many authors (*cf.* Mikuláš *et al.*, 2006; McLoughlin *et al.*, 2009; Rindsberg, 2012), but what specifically can be included within this is still being debated (Table 2; Rindsberg, 2012).

The criteria used to differentiate ichnotaxa are referred to as ichnotaxobases. Considering that trace fossils lack any evolutionary or genetic relationships, ichnotaxobases must be either morphological or inferred ethological criteria. Due to the inherent subjectivity of ethological classifications, ichnotaxobases must be based upon morphological criteria, the significance of which can be inferred through the perspective of ethology (Bromley, 1990, 1996; Knaust, 2012; Pickerill, 1994).

Classified as traces	**Not classified as traces**
Footprints, trackways	Any component part or representative stages of an organism (*e.g.*, bone, hair, egg)
Trails	
Burrows	
Borings	Calculi
Coprolites	Pearls
Gastroliths	Embedment structures
Regurgitaliths	Secreted cocoons
Nests	Plant reaction tissues (*e.g.*, plant galls)
Spider webs	Soils
Woven cocoons	Stromatolites
Caddis fly cases	Pathological structures (*i.e.*, signs of disease)
"Sand reefs"	
Signs of predation	
Signs of human biological activity	

Table 2. Various works of organisms which are either considered valid or invalid traces (Modified from Bertling *et al.*, 2006 and Rindsberg, 2012).

1.6.1 Morphometrics

Although ethological interpretations are a fundamental goal in ichnology (Buatois and Mángano, 2011; Knaust, 2012; Uchman, 1998), any inferred ethology is fundamentally subjective (Goldring *et al.*, 1997). Morphometrics are an attempt to objectively characterize morphology, studying not only dimensions, but their ratios (*e.g.* width to length); alternatively, measuring relative changes in various components (Rohlf and Markus, 1993). When describing trace fossils, morphometrics using as many criteria as possible are strongly encouraged (Bertling *et al.*, 2006). The use of morphometrics within a given trace assemblage can be useful in differentiating biodiversity from variations due to ontogeny. Exacting morphometrics have also been demonstrated as a valuable tool when analysing sediment-burrow interactions, in particular as related to reservoir characterization (Bednarz and McIlroy, 2012).

1.6.2 Valid Ichnotaxobases

Issues in the application of ichnotaxobases (*i.e.* what is a valid ichnotaxobase and for which taxonomic rank) have become more common throughout the literature and have yet to garner consensus (*cf.* Bromley, 1990, 1996; Pickerill, 1994; Bertling *et al.*, 2006 Bertling, 2007; Knaust, 2012). Considering ichnotaxobases are the criteria by which ichnotaxa are recognized, differentiated, and established, it is important that these distinguishing traits are both measureable and preservable (Bertling *et al.*, 2006). Labile

characteristics, those that are considered to be highly unlikely to be preserved or that would deteriorate quickly, should be avoided where possible (Bertling *et al.*, 2006). Characteristics that did not result from the life activity of the organism should also be avoided as an ichnotaxobase. Examples of this include geologic age, geographic location, structure of passive burrow fill, taphonomic alteration, and mode of preservation (Bertling *et al.*, 2006; Bertling 2007). Any inferred criteria, such as the tracemaker or related information (*e.g.* size, shape, or behaviour), are also unacceptable as ichnotaxobases (Goldring *et al.*, 1997; Bertling *et al.*, 2006; Bertling 2007). Certain morphological criteria, such as size, are less straightforward and their application is only suggested with caution at the ichnospecific level, and never at the ichnogeneric level (Bertling *et al.*, 2006, Bertling, 2007). Size alone is considered inadequate as an ichnotaxobase, as issues are likely to arise in characterizing various members of an ontogenetic group (Bertling *et al.*, 2006).

Only characteristics intrinsically related to the life activity which first modified the substrate should be used as ichnotaxobases. Although characteristics such as lithology are rejected, substrate (restricted to the principal types) can be used with caution (Bertling *et al.*, 2006). *Skolithos linearis* Haldeman and *Trypanites weisei* Mägdefrau are both valid ichnotaxa despite similar morphological expression, as different behaviour and body "tools" are required to produce them (Bertling *et al.*, 2006). In soft sediment an organism can displace or rearrange grains to form the required burrow morphology; however mechanical techniques or chemical abrasion is required in hard substrate (Bertling *et al.*, 2006).

Morphological ichnotaxobases are divided into different categories for ease in classification. 1) The general form, or overall shape, of an ichnotaxon includes elements such as the path (burrow or trail), arrangement/pattern, size (as described above), and branching; 2) the burrow boundaries, including the presence or absence of a burrow wall (including any ornamentation), lining, or mantle (*i.e.* an outer zone of burrow fill *sensu* Keighley and Pickerill, 1994) as well as whether it was actively or passively formed; 3) orientation with respect to substrate, which is considered a substantial differentiating characteristic; 4) active internal structure and/or fill (structure of passive fill is rejected as an ichnotaxobase), including meniscate backfill and spreite (Bromley, 1990, 1996; Pickerill 1994; Bertling *et al.*, 2006; Bertling, 2007).

Ichnology pertains to the life activity of all life that has ever existed, and as any fossilized trace from an animal or unknown origin is eligible to be described as an ichnotaxon, no universal approach to defining ichnotaxobases exisits. Ichnotaxobases should relate to intrinsic characteristics, but beyond that will require refinement by specialists in different areas of ichnology (Bertling *et al.*, 2006).

1.6.3 Ichnotaxobase hierarchy

Biotaxa share a common ancestry and each species holds a place within the tree of life. Cladistic schemes are created in attempting to understand evolutionary relationships. When conflict or disagreements arise within the created systems, biotaxa may be considered as *incertae sedis,* or of unknown placement. An inherent issue in

ichnotaxonomy is the lack of ancestry or relationship among traces, rendering all ichnotaxa *incertae sedis.* This creates an obvious issue with ichnotaxonomic ranking. The inconsistencies in the criteria (ichnotaxobases) that qualify to differentiate ichnogenera from ichnospecies are a substantial issue that requires resolution for ichnotaxonomy to progress (Schlirf and Uchman, 2005; Bertling *et al.*, 2006; Knaust, 2012).

Two competing ideologies have been proposed to provide stability and consistency in how ichnotaxobases are applied: 1) differentiating ichnotaxobases based on morphologies with inferred significance to ethology (Bertling *et al.*, 2006); 2) differentiating ichnotaxobases based on fundamental morphological elements and subsequent modifications thereof (Goldring *et al.*, 1997).

Although ethology is rejected for use as an ichnotaxobase, any morphological element that is considered to represent significant ethological differences should be used at the ichnogeneric level, and elements inferred to reflect minor ethological differences should be used at the ichnospecific level (Schlirf and Uchman, 2005; Bertling *et al.*, 2006). Wall linings, which are considered to represent a more substantial behaviour for horizontal burrows than for vertical burrows, are used to separate horizontal burrows at the ichnogenus level, but are used at the ichnospecies level for vertical burrows (Bertling *et al.*, 2006; Schlirf and Uchman, 2005; Boyd *et al.*, 2012). *Polykladichnus*, a vertically orientated burrow, can be lined or unlined (*P. irregularis* and *P. aragonensis* respectively), whereas despite the morphologically similar *Planolites* (unlined) and *Palaeophycus* (lined) are separated at the ichnogeneric level (Schlirf and Uchman, 2005). Branching is also inconsistently ranked as an ichnotaxobase as its importance is treated

differently in different burrow systems (Schlirf and Uchman, 2005). For example, *Skolithos* and *Polykladichnus* are vertical ichnogenera differentiated by branching, whereas several ichnogenera can either be branched or unbranched (e.g. *Arthrophycus*, *Oldhamia, Palaeophycus, Trichichnus*). Ethological methods of sorting ichnotaxobases is a logical approach, though it is fundamentally based on inferences and thus is inherently subjective (Goldring *et al.*, 1997).

Alternatively, ichnotaxobases can be sorted using primary and secondary morphological ichnotaxobases (Goldring *et al.*, 1997). Primary ichnotaxobases, those pertaining to the burrow segment occupied by the organism, are used for ichnogeneric differentiation, and secondary ichnotaxobases, those reflecting subsequent modifications are used at the ichnospecific level (Goldring *et al.*, 1997). Primary ichnotaxobases would include the cone and shaft, shaft and gallery, open burrow, footprint, etc. (Goldring *et al.*, 1997). Secondary ichnotaxobases include lateral displacement, branching, backfilling, etc. (Goldring *et al.*, 1997).

Recently, a third morphological approach to the hierarchy of ichnotaxobases identifies various elements and ranks their significance, placing them into an identification flow chart (Knaust, 2012). The proposed order of significance is: orientation (subvertical, subhorizontal, complex); branching; general shape (cylindrical, sinuous, lobate, spiral, radial, bifurcated, biserial, net-like, winding/meandering, U-shaped, J-shaped, dumbbell, boxwork, root-like); fill (passive or active); and burrow boundary (Knaust, 2012). While Knaust acknowledges that the classification is not perfect, it certainly has the potential to be a useful tool for ichnotaxonomy.

Ichnofamily designation is available to ichnotaxonomists, however very little has been written regarding their classification or how they should be employed. The few methods of characterization that have been proposed are summarized in table 3 (Bromley, 1996).

Ichnofamily	**Description**	**References**
Zooichnofamilies	Ichnotaxa based on the ethologies of a high taxon tracemaker	Rindsberg, 1994; Seilacher and Seilacher, 1994
Paraichnofamilies	Ichnotaxa that morphologically resemble their producer	Walter, 1983
Euichnofamilies	Ichnotaxa reflecting morphological and (interpreted) functional similarities of the trace fossil	Richter, 1926; Fu, 1991
Table 3. Methods of characterizing ichnofamilies (from Bromley, 1996).		

1.7 Near burrow sedimentary structures

Trace fossils are sedimentary structures which represent the life activity of an organism (or homotypic group of organisms) and as such, trace fossils could be named and classified in two possible ways: 1) as primary sedimentary structures; 2) more formally using binomial Latin names comparable to biotaxa (Bertling, 2007; Knaust, 2012). The convention of using the Linnaean system for nomenclature was made without purposeful consideration due to the early misidentification of many trace fossils as plants, which were then assigned a biological name by early palaeontologists (Bertling, 2007;

Bromley, 1990). As the traces themselves are biologically induced sedimentary structures, determining which near burrow sedimentary structures are related to the burrow and qualify for formal nomenclature can often be a challenge (Leaman *et al.*, 2015).

1.7.1 Structures that reflect ethology

The use of sedimentary structures as ichnotaxobases is argued against by several authors (Schlirf and Uchman, 2005; Bertling *et al.*, 2006; Bertling, 2007). When naming and characterizing biogenic structures, it is detractive to include abiotic components that do not reflect ethology. The delimitation of components that reflect ethology and those that do not can be a difficult task.

Following a study examining the burrowing strategy and mechanisms of maldanid polychaetes, they were proposed as the possible tracemaker of the ichnotaxa *Tasselia ordamensis* (Figure 2; Dufour *et al.*, 2008; Olivero *et al.*, 2010). *Tasselia ordamensis* had traditionally been interpreted as an equilibrium burrow created by a suspension feeder (D'Alessandro and Lannone, 1993; Wetzel and Bromley, 1996; Ponce *et al.*, 2007). The incipient (*sensu* Bromley and Fürsich, 1980) *T. ordamensis* produced by the maldanid polychaetes is the result of a complex suite of behaviours which involve head-down deposit-feeding, detritus feeding, and gardening (Dufour *et al.*, 2008; Olivero *et al.*, 2010). As the polychaetes deposit feed they ingest sediment from the bottom of the burrow and defecate the waste particles on the sediment-water interface (Dufour *et al.*, 2008; Olivero *et al.*, 2010). The pharynx of the organism has a limited capacity with

respect to grain size and as the organism feeds, it forms a biogenic graded bed (Rhoads and Stanley, 1965; Olivero *et al.*, 2010). As graded bedding is typically considered a primary sedimentary structure, it is generally rejected as an ichnotaxobase (*cf.* Bertling *et al.*, 2006, Bertling 2007). The graded bedding of *T. ordamensis*, however, is a direct reflection of the organism's physical characteristics (pharynx aperture) and its behaviour.

Sedimentary structures in the near-burrow environment are absent from the literature, outside of those advocating for its exclusion as an ichnotaxobase (Schlirf and Uchman, 2005; Bertling *et al.*, 2006; Bertling, 2007). These structures have the potential to yield valuable information that merits the expansion of the generally accepted ichnotaxobases to include more of the near-burrow environment. This discussion would not include any structure, feature, or trend that is of abiotic origin but should revolve around features that are biogenic, but are not currently accepted as criteria for diagnosis of ichnotaxa (e.g. burrow funnels).

A burrow funnel refers to the conical opening of a burrow as it meets the sediment-water interface. The vertically orientated cylindrical burrow *Monocraterion* Torell, 1870 is partially defined by the presence of an upper funnel-shaped aperture. Due to confusion surrounding a radiating component on the upper surface, the taxonomic status of *Monocraterion* is contentious (Schlirf and Uchman, 2005 for discussion). Additionally the funnel-shaped aperture is considered an unsuitable ichnotaxobase as it is easily eroded by seafloor processes (Schlirf and Uchman, 2005). It has also been suggested that *Skolithos* can also be found with a funnel-shaped aperture (Schlirf and Uchman, 2005), despite both the type material and type description lacking one

(Haldeman, 1840). Examination of the funnel-shaped aperture of *Monocraterion* demonstrates that, in at least some material, the cylindrical portion of the burrow extends into and crosscuts the funnel portion, demonstrating that the organism inhabited the burrow during, and was potentially responsible for, the surrounding sediment collapse (Figure 3; McIlroy and Garton, 2010). The rejection of all funnel-shaped apertures on the basis that some may be created abiologically, when many can be demonstrated as having been inhabited during the sediment collapse and are thus probably formed intentionally, is not beneficial.

Sediment collapse structures are well documented in association with various ichnotaxa, including *Ophiomorpha* and *Thalassinoides* (Figure 4; Buck and Goldring, 2003; Leaman *et al.,* 2015). Neoichnological experimentation has documented the creation of collapse cone structures as a method of sediment transport into burrow galleries for feeding and/or acquisition of building materials (Figure 5; Leaman *et al.,* 2015). Similar structures have been observed associated with *Diplocraterion* which are also inferred to have been created for feeding (Leaman et al. in press). Seven scenarios have been identified that lead to sediment collapse structures under varying conditions (Buck and Goldring, 2003):

> "1) sand collapse into a cavity (decomposed body, open shaft, or gallery), (2) upward (escape) or downward locomotion by an organism through the sediment, (3) upward adjustment (equilibration), (4) casting of coelenterates' excavations, (5) organism-mediated soft-sediment deformation in heterolithic sediment, (6) biodeformational small and large excavations by organisms, and (7) fluid (gas or liquid) escape structures" –Buck and Goldring, 2003

This study determined criteria that aid in the distinction of the cause of the collapse (Buck and Goldring, 2003). Although collapse structures are commonly thought of as sedimentary structures, they are often associated with biogenic structures and a biogenic mode of formation can often be determined by examining the collapse morphology and its associations (Buck and Goldring; 2003; Leaman et al., 2015). Considering these structures are morphologically recurrent modifications of substrate as a result of the life activity of an organism, their inclusion as an ichnotaxobase has potential to aid in the characterization of trace fossils and with ethological studies.

Some authors have expressed concern regarding the preservation potential required for a structure to be a valid ichnotaxobase, which would include funnel-shaped apertures and sediment collapse structures (Schlirf and Uchman, 2005; Bertling *et al.*, 2006; Bertling, 2007). Should numerous fossil examples be found, and given their potentially ethological origin, these structures should be considered when describing ichnotaxa. The preservation potential alone should not be grounds for rejection of a structure or characteristic as an ichnotaxobase as this has the potential to eliminate valuable data. If a criterion with low preservation potential is maintained as an ichnotaxobasis to delimit an ichnospecies or ichnosubspecies, the worker has the ability to gain the additional information should it be observed. In the interest of stability, criteria with low preservation potential should only be considered at the ichnospecific or ichnosubspecific level.

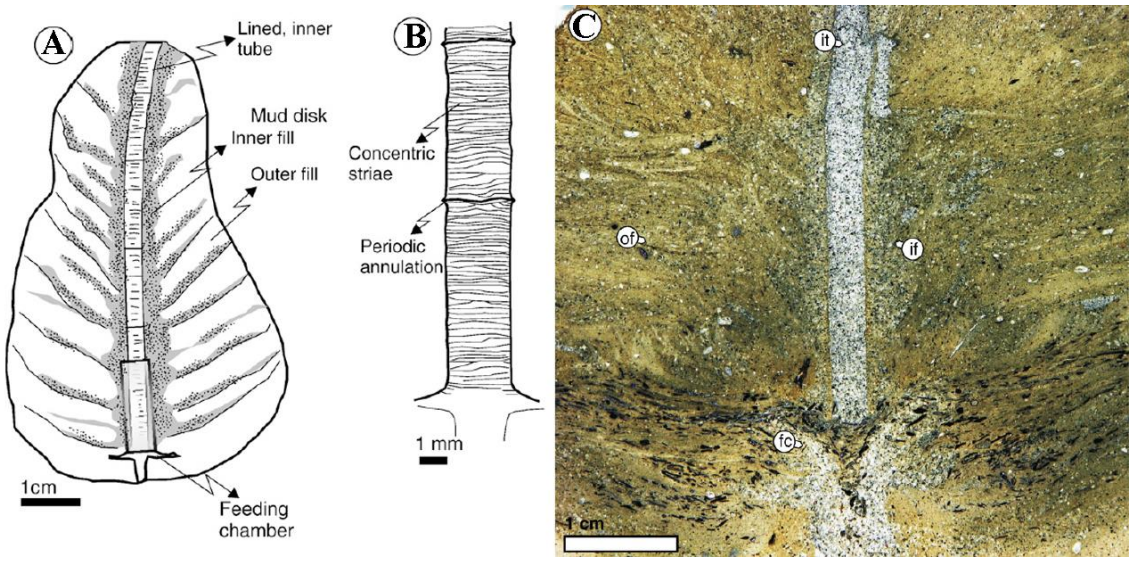

Figure 2. A-B) Sketch showing morphologic components of *Tasselia ordamensis* C) Biogenic graded bedded inferred to have been produced by a maldanid polychaete-like organism (modified from Olivero *et al.*, 2010)

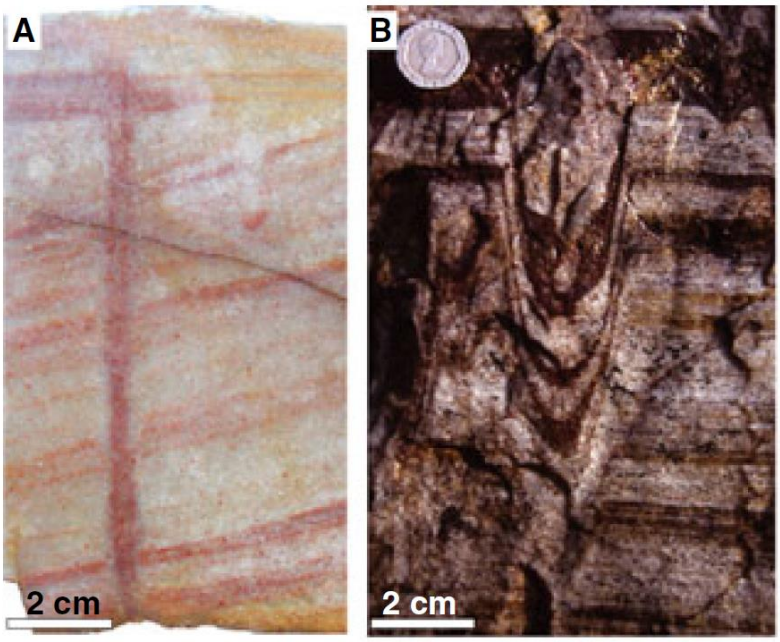

Figure 3. *Skolithos* burrow (A) compared with *Monocraterion* displaying funnel-shaped aperture (B) (from McIlroy and Garton, 2010)

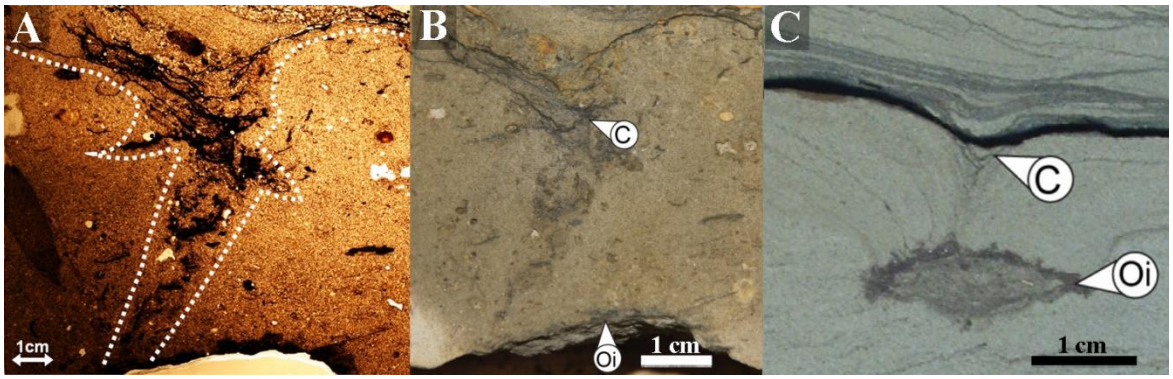

Figure 4. Collapse cones in relation to *Ophiomorpha* and *Thalassinoides* A) Collapse structure in association to an *Ophiomorpha* and *Thalassinoides.* Dotted white line approximately delimits the collapse structure (courtesy of Daniel Niquet); Collapse cone (icon labeled c) in association to *Ophiomorpha irregulaire* (Oi) from offshore Newfoundland (B) and offshore Norway (C) (Modified from McIlroy 2004b; Leaman *et al.*, 2015).

Figure 5. A) *Neotrypaea californiensis* burrow, producing an incipient *Ophiomorpha irregulaire* burrow with lined burrow roof, and collapse cone (C); B) *Neotrypaea californiensis* feeding beneath a collapse cone (Modified from Leaman *et al.*, 2015).

1.7.2 Non-ethological sedimentary features

Abiogenic sedimentary structures are commonly directly associated with trace fossils. *Skolithos musicalis* was introduced for a burrow that included sedimentary structures between the vertical tubes as the key diagnostic characteristic of the ichnospecies (Schallreuther and Hinz-Schallreuther, 2003), but has subsequently been rejected on the basis that the sedimentary structures between the burrows are not considered a valid ichnotaxobase (Schlirf and Uchman, 2005). Vertebrate footprints are often associated with undertracks (depressions of the sediment beneath the footprint), which only reflect local rheological information rather than any ethological information (Manning 2004; Milan and Bromley, 2006). Any sedimentary structure that does not reflect information pertaining to the formation of the trace must be rejected as an ichnotaxobase. This would include ripples, crossbedding, desiccation cracks, and any other primary sedimentary structure. Specific criteria have been suggested to facilitate this process, although they are not meant to act as a strict checklist; used collectively they provide a practical guide (Table 4; Pickerill, 1994).

Although non-ethological sedimentary structures cannot be used as an ichnotaxobase, their presence and association with various traces should be documented. An ichnologist working to understand these fossilized structures, behaviours, and by extension palaeoenvironmental conditions, should be careful not to overlook information present in the sedimentary/geological record as it can potentially lead to a more complete understanding of the ichnological record.

Evidence for ethological origin	Evidence for abiotic origin
Uniform size and/or continuity of an individual structure	Resemblance to a primary inorganic sedimentary structure
Regular, complex and repetive geometric form	Resemblance to a secondary diagenetic structure
Lining or wall structure	Variable or tapering dimensions
Spreite or meniscate fill	Non-uniform size and or shape of multiple structures
Pellets or an organic residue	Irregular geometric pattern
Very delicate morphologic features	Strict preferred orientation
Preservation in full relief	Obvious mineral replacement
Preservation of a body fossil in direct association with the structure	

Table 4. Criteria for distinguishing ethological versus non-ethological structures (Modified from Pickerill, 1994)

2. Thesis Objectives

Recent studies involving three-dimensional morphological reconstructions of various trace fossils have highlighted that prior to complete three-dimensional characterization, these structures are rarely fully understood (*e.g.*, Bednarz and McIlroy, 2009; 2012; Boyd *et al.*, 2012; Bednarz *et al.*, 2015; Leaman *et al.*, 2015). This study aims to characterize the well preserved shoreface ichnological assemblage of the Carboniferous heterolithic silt and sandstone deposits near Howick, Northumberland in the United Kingdom. Additional aims include further developing and refining the

modelling techniques laid out in Bednarz *et al.,* (2015) to achieve greater preservation of lithological data and achieve more accurate digital models. Particular focus is given to three prominent ichnotaxa which are in need of detailed examination: *Dactyloidites jordii* isp. nov., *Beaconites capronus*, and *Neoeione moniliformis* igen. nov., comb. nov. (Chapters 2-4 respectively).

2.1 Aims and objectives of CHAPTER TWO

Chapter two reviews the ichnogenus *Dactyloidites* and introduces the new ichnospecies *D. jordii.* Specimens were collected from closely localized float and processed using petrographic techniques, X-ray diffraction, and serial grinding/photography to produce a high-resolution three-dimensional model. *Dactyloidites jordii* isp. nov. is compared to the morphologically similar ichnospecies *Dactyloidites ottoi* and *D. peniculus*. The complex three-dimensional morphology of the *D. jordii* burrow system was noted in the field prior to sample collection. These burrows form relatively large, multitiered, stellate to palmate structures composed of a large number of radiating branches. The probes of the burrow tend to follow a programmed pattern; however, the burrow design is altered upon encountering non-ideal conditions. The resultant variation highlights the need for ichnologists to provide a type series rather than a single holotype in order to capture the broad range in burrow morphologies. The complex burrow morphology and the inherent range in morphology, reflecting the adaptive nature in burrow construction of the tracemaker are assessed in high resolution and forms the basis for the palaeobiological and ethological analysis.

2.2 Aims and objectives of CHAPTER THREE

Chapter three aims to fully characterize and document the prevalent winding meniscate back-filled trace *Beaconites capronus*. *Beaconites* burrows are differentiated from other meniscate back-filled burrows *Taenidium* and *Ancorichnus* by the presence of a simple, yet prominent, burrow lining lacking ornamentation. *Taenidium* lacks, or has a minimal, burrowing lining; whereas *Ancorichnus* display a mantle (*i.e.*, an outer zone of burrow fill; *sensu* Keighley and Pickerill, 1994).

The *B. capronus* of the Howick succession are commonly associated with vertical pipes whose form is morphologically identical to that of the horizontal sections of the burrow system. As these vertical components are also actively back-filled, the tracemaking organism would have been isolated from the sediment-water interface, exposing the organism to low-oxygen porewater. Samples of *B. capronus* are studied herein in high-resolution three-dimensional models assessing the connection between the horizontal winding portions, and the backfilled vertical tubes. While the *B. capronus* burrows assessed for this study do not tend to self-cross, they do regularly demonstrate secondary successive branching (*sensu* D'Alessandro and Bromley, 1987). These distinct morphological elements are analysed to provide insight into the potential palaeobiological and ethological mode of burrow construction.

2.3 Aims and objectives of CHAPTER FOUR

Chapter four aims to review burrows that Tate (1859) originally introduced as *Eione moniliformis* and incorrectly considered as a fossil example of an annelid. The name *Eione* however, had been previously used for a genus of gastropod (Rafinesque, 1814),

making *Eione,* Tate a junior homonym of *Eione* Rafinesque. Attempting to correct this, Buckman (2001) created a new ichnogenus to accommodate burrows composed of two distinct layers, and transferred *Eione moniliformis* to *Parataenidium*. This study aims to clarify the current taxonomic status of *Parataenidium moniliformis* as well as to provide an updated ethological model for the burrow construction. This study also aims to elucidate the probable type locality for *N. moniliformis* and the neotype material designated by Buckman (2001).

2.4 Aims and objectives of CHAPTER FIVE

Chapter five aims to provide a systematic analysis of the ichnological assemblage in the coastal outcrop of the Stainmore Formation located near Howick, Northumberland. A systematic field study was carried out using photographs, and analysis of samples collected from closely localised float. Several samples were serially ground and photographed to assess complex ichnotaxa.

3. Methodology

The methodology and analytical approaches employed in this study are a combination of established and novel techniques. These include the serial grinding and photographic modelling techniques examined in Bednarz *et al.* (2015; *cf.* appendix A), field assessment and sample collection/characterization (including the use of X-ray

diffraction), and petrographic analysis (including automated porosity calculation using petrographic images; *cf.* appendix B).

3.1 Serial grinding and photographic digital modelling

An objective of this study is to build upon the techniques employed by Bednarz and McIlroy (2009), and later refined in Bednarz *et al.* (2015; appendix A). This method involves encasing a sample in plaster and squaring the edges which will later act as a constant frame of reference. The sample is then placed within an automated computer guided milling machine. The machine is equipped with a diamond carbide grinding tool traditionally used for hard metal processing. After the initial surface of the sample is registered within the machine the grinding head is lowered by a precise increment depending on the desired resolution; the samples processed in this study used a grinding interval of *c.* 0.1 mm. After the grinding tool has passed over the entire sample, the specimen is removed from the machine and photographed under constant lighting conditions in a dedicated photography lab. The photography setup involves the sample being laid on its side on a glossy white backdrop with the exposed face of the sample facing outward towards a high-resolution, remote controlled, digital single-lens reflex camera. The freshly ground surface is aligned on the backdrop, maintaining a constant distance from the camera sensor. The sample is photographed both dry and wetted with oil to enhance the colour contrast and clarity of the exposed sample surface. The sample is then returned to the milling machine where it is restrained using a precision clamp, ensuring the sample returns to the same place on the milling machine table. This process

is repeated until the entire sample is ground and photographed, or the structure of interest has been completely processed. This process produces a series of hundreds of images, depending on the sample size and resolution of the grinding increment. These images are then processed in photo-manipulation software to ensure consistent colour and exposure of each image. These edited images are imported into a digital stack (*i.e.* a single digital file containing multiple layers of images) within the software Adobe Photoshop®. Each image is meticulously aligned using the square corners of the plaster block encasing the sample as the constant frame of reference. After the photographs are aligned specific features of interest are digitally extracted using a variety of methods. 1) The structure of interest is selected using an automated selection algorithm based on colour contrast of surrounding pixels (the 'magic wand' toolset within Photoshop®) and copied into a new layer. 2) A selection brush is used to mark an area which is selected and then copied to a new layer (the 'quick select' toolset within Photoshop®). 3) Elements of interest are directly traced onto a new layer using a pen or marker tool. This process creates an additional stack of images containing only the extracted feature of interest that is displayed over a solid black or white background. Using scale images the pixel dimensions are calculated (*i.e.* the physical distance across the specimen that is represented in each pixel). The pixel dimensions are then used to calculate the voxel dimensions used in the modelling process (A voxel is a three dimensional 'pixel' with dimensions X, Y, and Z. X and Y are calculated from the pixel dimensions and Z is the grinding interval). This stack of extracted images is imported into volume graphic software that renders the images as a solid three dimensional object (*e.g.* VGStudio Max ®). The resultant high-resolution digital model is highly accurate, and can be manipulated

or cross-sectioned in any plane. Additional rendering algorithms are available with the volume graphic software that is capable of producing renderings of external and internal structures (comparable to an X-radiograph image).

3.1.1 Improvements on the basic technique

While completing this study several improvements have been made to the techniques explained above. Formerly the serial grinding images are processed monochromatically producing colourless digital models that can then be false coloured. By improving the consistency in the lighting and editing of the serial grinding images, true colour models were produced using full-colour images. These true-colour models allow for easy visualization of any lithological information represented by the rock colour (e.g. sandstones versus mudstone). Additionally, using improved computers, larger digital models and combinations of separate structures were rendered individually within a given model. This allows for the ability to turn on and off specific components of a burrow system for easy visualization of distinct components in digitally ‘crowded’ areas of the model.

The digital selection and extraction of burrow components is often challenging when considering a three-dimensional structure and making selections from two-dimensional images. This is particularly challenging when the burrow morphology is complex or poorly understood. In order to have a better idea of which structures to include in a model, the whole rock images were imported and modelled using the volume graphic software. The resultant whole-rock model is comparable to a computerized tomography image that can be dissected in any plane and rendered to gain early insight in

related structural components. Additionally, this method of whole-rock modelling allows for easy visualization of sedimentary structures relating to a burrow that may be difficult to extract from the overall image (e.g. conical collapse structures, sediment lamination, etc.).

3.2 Field assessment and sample collection/characterization

Samples for this study were collected from closely localized float from the coastal cliffs near Howick. Approximately 4.5 m of succession were logged analytically at the cm scale as well as using a series of high-resolution digital images which were aligned to form both lateral panoramic and vertical photo-logs of the succession. The ichnological diversity was noted and photographed. The succession is composed in interbedded sandstone and fine grain siltstone/mudstone. X-ray diffraction was used to determine the likely mineralogical composition of the clays present throughout the samples and succession.

4. Study Area

Samples for this study were collected from the coastal cliffs near Howick, Northumberland in the United Kingdom. The age of the succession is Bashkirian and is within the Milestone Grit unit of the Stainmore Formation (within the Yordale Group;

Dean *et al.*, 2011). The Stainmore Formation is typically composed of interbedded sandstone, siltstone, mudstone, and limestone (Dean *et al.*, 2011). It is considered to represent various marine through deltaic cycles (Dean *et al.*, 2011).

All of the samples examined for this study were collected from an approximately 4.5 m thick succession within a small cove located at 55°27′30.38″N, 1°35′34.32″W. This outcrop displays excellent preservation of various trace fossils dispersed throughout the inter-bedded sandstone and siltstone beds that range in size from cm to dm in thickness. Bioturbation generally ranges from 5-20% with localised zones of intense bioturbation, approximately 90%, within clay-rich mudstone beds. The succession displays a net upward-coarsening trend and is composed of several upward-coarsening parasequences. The clean sandstone units often exhibit trough cross-bedding as well as hummocky cross-stratification. This succession is inferred to have been deposited between the fair-weather wave base and storm wave base, as a part of a storm-dominated marine shoreface.

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CHAPTER TWO

Three-dimensional morphology and palaeobiology of the trace fossil *Dactyloidites jordii* isp. nov. from the Carboniferous of England.

(In review with Geobios)

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KEYWORDS

Dactyloidites; Serial-grinding; three-dimensional reconstruction; ichnology; Stainmore Formation; ichnotaxonomy

*This chapter is formatted according to the standards set by *Geobios*

Abstract

The diverse ichnological assemblage from the outcrops near Howick, Northumberland United Kingdom, is exceptionally well preserved. Among these Carboniferous ichnotaxa is a new ichnospecies of *Dactyloidites*. Specimens were collected and processed using high-resolution serial grinding and photography to produce an accurate and precise three-dimensional model of these new burrows in full colour. The model produced in association with petrographic thin sections and field observations is used as the basis for comparison between *Dactyloidites jordii* isp. nov. and other ichnospecies of *Dactyloidites*. The current taxonomic status of the ichnogenus is examined and reviewed. *Dactyloidites jordii* isp. nov. is a broadly bisymmetrical, stellate to palmate burrow composed of numerous long, narrow rays that exhibit three orders of branching arranged into tiered galleries radiating from a central shaft. The trace maker is suggested to be a vermiform organism with an adaptive burrowing strategy that facilitates alteration of its burrow construction to accommodate suboptimal sediment conditions. The adaptive nature of trace-making organisms and the inherent anisotropy of many burrowed media highlight the need for ichnologists to provide a type series rather than a single holotype, in order to capture the inherent range of common burrow morphologies.

1. Introduction

Exceptionally well-preserved stellate trace fossils of the ichnogenus *Dactyloidites* from the interbedded sandstones and siltstones of the Carboniferous Stainmore Formation of the Yoredale Group in Northumberland, United Kingdom (Fig. 1) were investigated using serial grinding and three-dimensional reconstruction (cf. Bednarz and McIlroy, 2009; Boyd et al., 2012; Bednarz et al., 2015). The detailed reconstructions allow consideration of the bauplan for the construction of the ichnogenus *Dactyloidites* Hall, 1886. The modelling approach employed herein, when integrated with field observations and petrographic analysis, allows the trace fossil to be considered within the context of the surrounding sediment.

The ichnogenus *Dactyloidites*, like many of the radiating trace fossil taxa, has a complex taxonomic history and is in need of thorough revision. This paper aims to summarize the current ichnotaxonomic status of *Dactyloidites* and to consider the present material within that framework. Outside the material presented herein are four valid ichnospecies: *D. asteroides* Fitch, 1850, *D. cabanasi* (Meléndez in Cabanás, 1966), *D. ottoi* (Geinitz, 1849), and *D. peniculus* (D'Alessandro and Bromley, 1986). As both *D. asteroides* and *D. cabanasi* differ significantly from *D. ottoi* and *D. peniculus*, our material is compared only with the more similar *D. ottoi* and *D. peniculus.*

Dactyloidites is found in interbedded siltstones and sandstones that range from centimeter to decimeter in thickness. The Stainmore Formation shows net upward coarsening, and is composed of several upward-coarsening parasequences. The

Dactyloidites-bearing part of the succession consists of clean sandstones with hummocky cross stratification interbedded with micaceous siltstones in which bioturbation generally ranges from 5 to 20%, except for rare, highly bioturbated mudstones that are upwards of 90% bioturbated. The depositional setting is inferred to have been that of a storm-dominated marine shoreface, with the *Dactyloidites* being found in strata deposited below the fair-weather wave base, but above the storm wave base (Fig. 2).

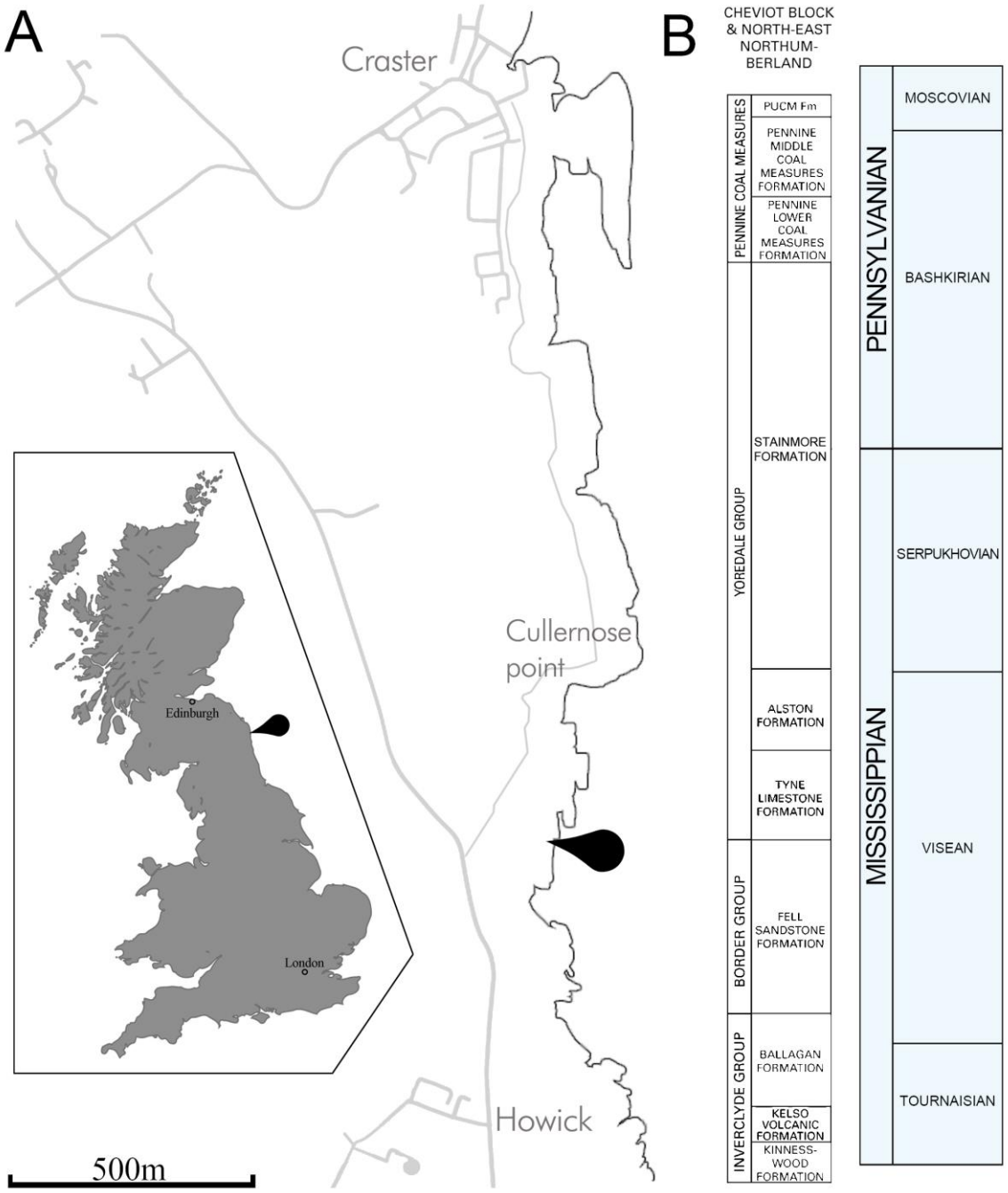

FIGURE 1. A) Map of field location and sample location (55° 27′30.38″N, 1° 35′34.32″W) on the coast between Howick and Craster. The inset identifies the field location within the United Kingdom; B) Generalised stratigraphic column showing the Stainmore Formation in relation to the Yoredale Group and others from North-East Northumberland. Modified from Dean et al. (2011).

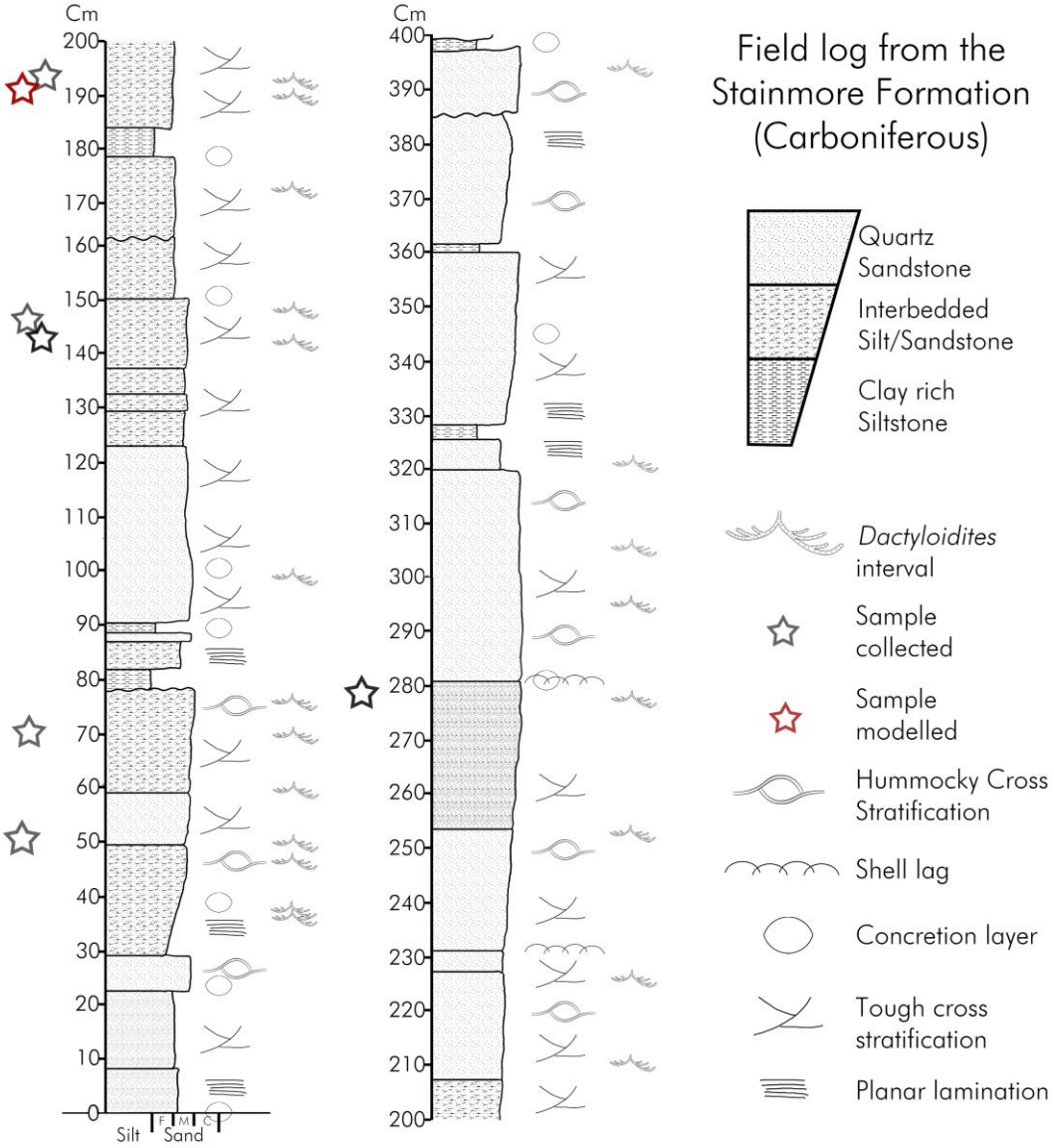

FIGURE 2. Sedimentary field log of the Stainmore Formation located near the town of Howick, Northumberland (55° 27′30.38″N, 1° 35′34.32″W). The stars indicate the location where *Dactyloidites* specimens were collected.

2. Methodology

Eight field samples were collected and analysed for this study using the serial grinding and photographic methods developed by Bednarz et al. (2015). This method involves encasing the samples in plaster and then sequentially removing minute increments using a computer-guided milling machine with an abrading tool. The grind increment used in this study was 0.3 mm. After each increment was ground, the sample surface was coated with oil, to enhance colour contrast, and photographed under controlled conditions. The stack of photographs was then image-processed and aligned using Adobe Photoshop. The features of interest were then extracted from the images and modelled using the volume graphic software VG Studio Max (Fig. 3). All images were left in full colour so as to facilitate visualization of any feature within the volume in its natural lithological expression. The resultant high-resolution interactive models can be digitally cross-sectioned in any plane as well as rendered partially transparent to facilitate morphological and morphometric analysis (see supplementary materials for interactive model). The three-dimensional model allows examination of burrow morphology (e.g. branching characteristics) that is difficult to achieve in a hand-sample. Modelling the fossil burrows and the host sediment importantly allows consideration of the interaction between the trace fossils and adjacent strata, which can be invaluable to improve palaeobiological understanding of organism-sediment interactions in three dimensions.

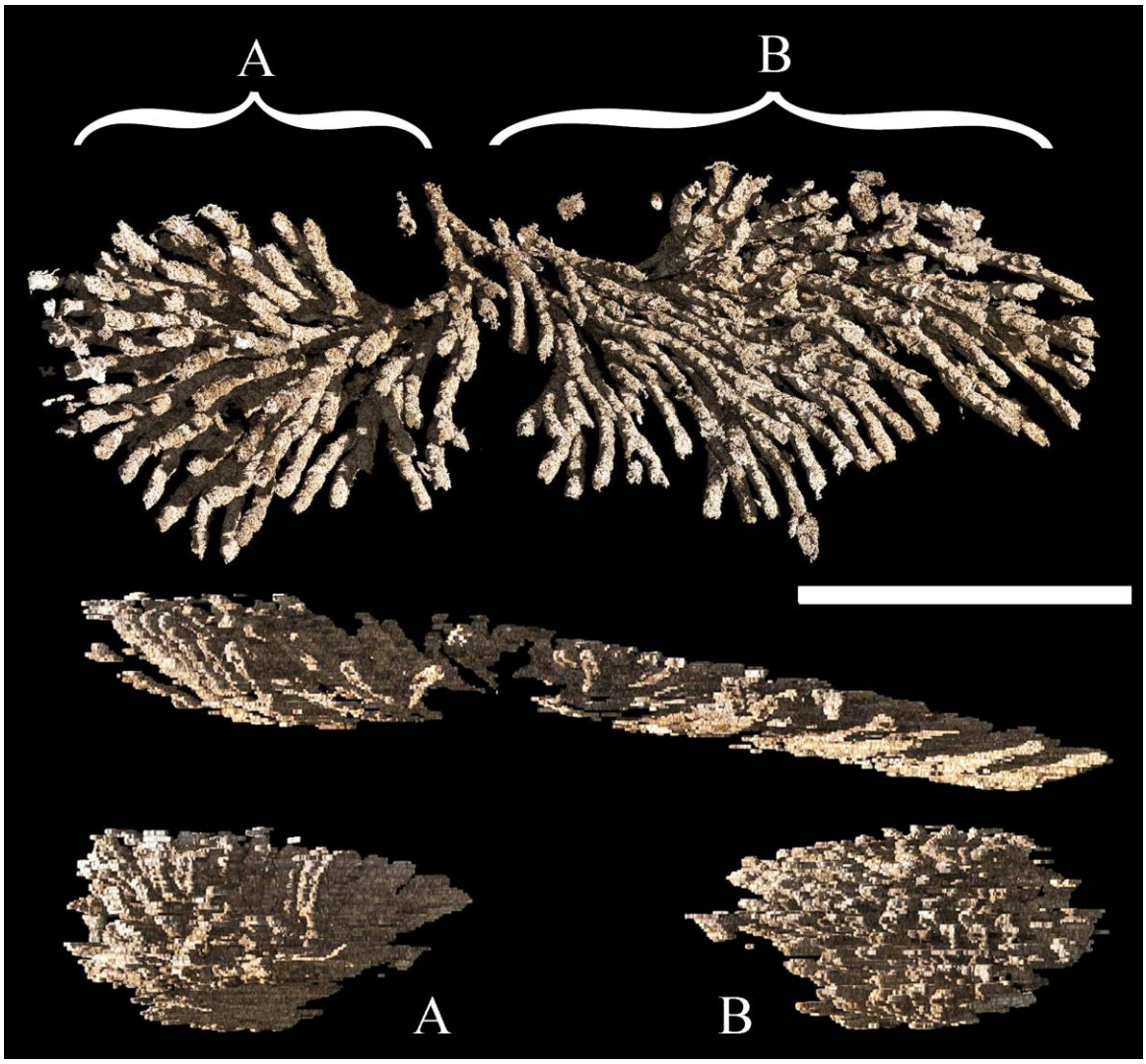

FIGURE 3. Digital model of *Dactyloidites jordii* viewed from all sides, in true colour.

Burrow is divided into two portions denoted by the letters A and B. Scale bar: 5 cm.

3. Systematic ichnology

Ichnogenus *Dactyloidites* Hall, 1886

Type ichnospecies: *Buthotrephis asteroides* (Fitch, 1850); lower Cambrian, New York State, USA.

Emended diagnosis: Mid-to-deep burrow system forming stellate to palmate rosettes composed of branched or unbranched actively filled spreite-bearing branches radiating horizontally to sub-horizontally from a single vertical to sub-vertical central shaft.

Remarks: The ichnogenus *Dactyloidites* Hall, 1886 has a complicated taxonomic history and has undergone numerous significant revisions (Walcott, 1898; Häntzschel, 1970, 1975; Fürsich and Bromley, 1985; D'Alessandro and Bromley, 1986; Vyalov, 1989; Schweigert, 1998; Ciampaglio et al., 2006; Uchman and Pervesler, 2007; Wilmsen and Niebuhr, 2013). The type ichnospecies, *Dactyloidites asteroides,* was originally introduced as the fossil alga, *Buthotrephis asteroides* Fitch, 1850. The type material of *Buthotrephis asteroides* is considered as junior synonyms of pre-existing ichnospecies of *Chondrites,* and as such *B. asteroides* needed to be reassigned to another ichnogenus (Fillion and Pickerill, 1990). The ichnogenus *Dactyloidites* was introduced as an unknown body fossil, and was considered to be a fucoid algae or a sponge (Hall, 1886). The type species, *Dactyloidites bulbosus*, was synonymized with *Buthotrephis asteroides* (Walcott, 1898), but since *B. asteroides* had priority—and the genus *Buthotrephis* was invalid—this structure was assigned to *Dactyloidites* Hall, 1886, and *D. bulbosus* became

a junior synonym of *D. asteroides* (Walcott, 1898). Walcott (1898) designated the original material of Fitch (1850) as the type specimen of *Dactyloidites asteroides* (Walcott, 1898). Fürsich and Bromley (1985) reviewed *Dactyloidites* and synonymized *Haentzschelinia* Vyalov, 1964 and *Brooksella* Walcott, 1896 with *Dactyloidites*, and considered three ichnospecies; *D. canyonensis*, *D. ottoi*, and *D. asteroides*, to be valid.

The radiating structure *Brooksella* is superficially similar to *Dactyloidites*, and is known from two species, *B. alternata* Walcott, 1896 and *B. confusa* Walcott, 1896, which were introduced along with the genus *Laotira* Walcott, 1896. *Laotira cambria* (the sole species of *Laotira*) and *B. confusa* were later considered as junior synonyms of *Brooksella alternata* Walcott, 1896 (Willoughby and Robinson, 1979; Ciampaglio et al., 2006). Three-dimensional CT tomographic examination of *B. alternata* has demonstrated that the type material consists of body fossils of a protospongiid poriferan, and as such cannot be synonymized with *Dactyloidites* (Ciampaglio et al., 2006). *Brooksella canyonensis* (Bassler, 1941), which was originally considered to be a jellyfish, has subsequently been: 1) reinterpreted first as a gas escape structure (Cloud, 1960); 2) considered to belong to the trace fossil *Asterosoma* von Otto, 1854 (Glaessner, 1969); 3) synonymized with *Dactyloidites* (Fürsich and Bromley, 1985); and 4) considered to be a pseudofossil (Runnegar and Fedonkin, 1992). The pseudofossil interpretation is tentatively supported herein based on study of morphologically comparable fluid escape structures associated with microbial matgrounds (Menon et al., in press). The issue of the taxonomic position and biogenicity of *B. canyonensis* requires re-examination of the type material to look for evidence of underlying fluid escape structures.

The radiating ichnogenus *Haentzschelinia* was created in 1964 with two ichnospecies, *H. kolymensis* Vyalov, 1964 and *H. pygmea* Vyalov, 1964, with a third ichnospecies being added following reinterpretation of the sponge *Spongia ottoi* Geinitz, 1849 as a radiating trace fossil (Häntzschel, 1970). When *Haentzschelinia* was synonymized with *Dactyloidites* all three ichnospecies were synonymized and the oldest name, *Dactyloidites* (formerly *Spongia*) *ottoi*, took priority (Fürsich and Bromley, 1985). This synonymization has, however, been contested by some authors (Vyalov, 1989; Schweigert, 1998). Reconsideration of the status of *Haentzschelinia kolymensis* and *H. pygmea* is made problematic by the loss of the type material, but from examination of photographs, they are both tentatively placed in synonymy with *D. ottoi* (Fürsich and Bromley, 1985).

Two more recent ichnospecies of *Dactyloidite*s are: 1) *Anthoichnites cabanasi* Meléndez in Cabanás, 1966 which has recently been transferred to *D. cabanasi* (Gámez Vintaned et al., 2006); and 2) *D. peniculus* D'Alessandro and Bromley, 1986, whose diagnosis was subsequently emended (Uchman and Pervesler, 2007).

Ichnospecies *Dactyloidites jordii* isp. nov.

Figs. 3-9

Derivation of the name: The name *Dactyloidites jordii* honours the work of the late Dr. Jordi María de Gibert.

Type material: We hereby designate two specimens as syntype material as well as two syntype petrographic thin sections. Sample (*NFM F-997*) and slides (*NFM F-996.1* and *NFM F-996.2*) are currently being housed in the care of The Rooms, Provincial Museum of Newfoundland. Due to the destructive nature of our analysis, the physical syntype material of "UKH-3" no longer exists. In accordance with ICZN article 73.1.4 we maintain its utility as a syntype and the 86 digital raw images used in processing the above model are included herein as digi-syntype material (*sensu* Adams et al., 2010).

Type locality: The type series was collected from the Bashkirian Stainmore Formation, in coastal cliffs near Howick, Northumberland, United Kingdom (55° 27'30.38"N, 1° 35'34.32"W; Figs. 1, 2).

Material: 8 specimens (destructive analysis of one of which produced a high-resolution three-dimensional model presented herein); 4 thin sections.

Diagnosis: Broadly bisymmetrical trace fossil consisting of narrow radiating burrows that fan out between 70^{o}–180^{o} degrees on each side of a central shaft that is orientated oblique to bedding. The burrows may exhibit multiple orders of primary successive branching within a fan, with several fans being arranged in successive tiers that are laterally oblique to one another. The component burrows can branch both horizontally and vertically.

Description: The specimen chosen to be modelled in three dimensions measures 203.0 mm by 67.4 mm across and is 25.8 mm deep (Fig. 3), and is composed of two radiating portions that diverge from a central burrow that bifurcates to create the two

broadly symmetrical halves of the trace (Fig. 3). The complete trace fossil is composed of approximately one hundred and forty four radiating burrows, consisting of approximately sixty in portion A, and approximately eighty four in portion B. The branches of *D. jordii* become progressively more steeply inclined with each consecutive branch. Burrow diameter and angle of inclination were measured throughout the specimen using eighty burrow segments for the diameter and twenty seven point measurements for the angle of inclination (Table 1). Burrow segments in section A have an average burrow diameter of 2.42 mm, with a standard deviation of 0.34. The average angle of inclination of the tubes in section A is 13.3^{o} close to the primary branching point, and 29.9^{o} distally, with a mean of 25.9^{o}. Tubes in section B have an average burrow diameter of 2.60 mm, with a standard deviation of 0.31 mm. The average angle of inclination of tubes in this section is 10.63^{o} close to the primary branching point and 13.6^{o} distally, with a mean angle of inclination of 12.2^{o}. Transverse cross sections of the burrow probes often exhibit an 'n'-like morphology (Fig. 4)

Both sides of the specimen show multiple orders of branching, demonstrating in excess of four orders of vertical and horizontal oriented primary successive branching (ie. when an organism actively fills a systematically branched structure, sensu D'Alessandro and Bromley, 1987) . The two sides of the reconstructed burrow differ in that: in section A the initial branch is the longest and deepest branch, with subsequent branches being more proximal to the primary branching point; and in section B the branching is less regular and subsequent orders of branching form progressively deeper tiers of the structure (Fig. 3). The different burrowing "program" in section B is considered to be due

to the trace maker interacting with an erosional sediment-sediment contact (Fig. 5). The erosional contact and overlying sediment pre-date the burrow, as demonstrated by the disruption of sedimentary laminae above burrow terminations (Fig. 5). *Dactyloidites* is composed of fine- to medium-grained quartz sand with low clay content. X-ray diffraction demonstrates that the burrows have a mica- and clay-rich lining approximately 0.2–0.5 mm thick (average 0.3 mm) that is composed predominantly of illite, chlorite, and biotite. The grains making up the lining are oriented parallel to the tube (Fig. 6).

TABLE 1 – Morphometrics of *Dactyloidites jordii* isp. nov.

Section	Average angle	Proximal angle	Distal angle	Total numbers of Probes	Diameter	Max/Min
A	25.89°	13.29°	29.9°	60+	2.4 mm	3.1/1.7 mm
B	12.22°	10.63°	13.36°	84+	2.6 mm	3.2/1.8 mm

Remarks: *Dactyloidites jordii* isp. nov. is morphologically similar to *D. ottoi* and *D. peniculus*, but differs in that the radial tubes of *D. jordii* have many unilateral serial branches that are usually narrower (1.5–3.5 mm) than those of both *D. ottoi* (4–6 mm) and *D. peniculus* (4–5 mm). *Dactyloidites peniculus* and *D. jordii* can have comparable high numbers of radiating burrow probes, however, the causative burrows in *D. peniculus* form tight clusters of unbranched probes which often overlapping, whereas in *D. jordii* the branched burrows are evenly separated and do not self-cross. The prominent lining associated with the probes also differentiates *D. jordii* from those of *D. ottoi* and *D. peniculus* (Fig. 7). *Dactyloidites jordii* also differs from *D. ottoi* and *D. peniculus* in being bisymmetrical, and having incomplete rosettes of burrows that range from 70^{o}–180^{o},

whereas the radial portion of other ichnospecies of *Dactyloidites* usually radiate over 200^{o}.

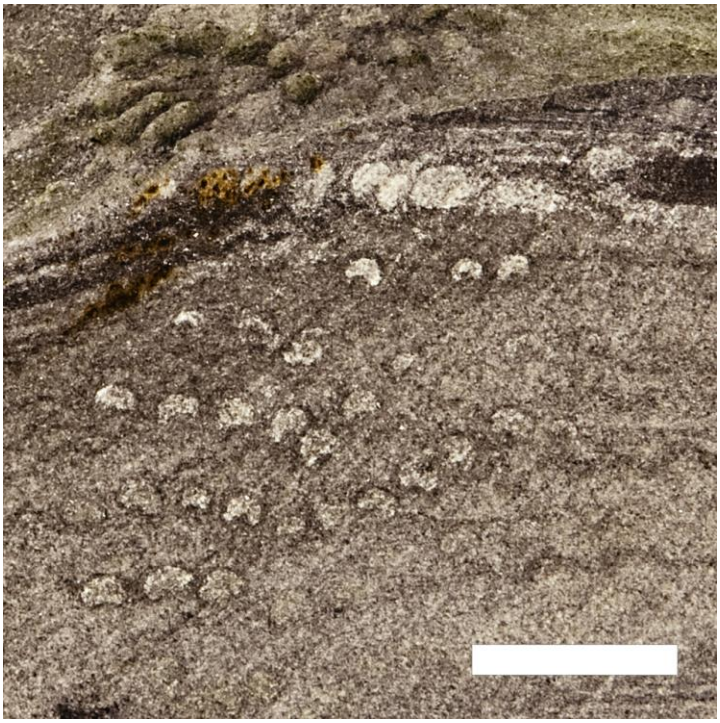

FIGURE 4. Transverse cross section through the tiered fans of burrows that make up *Dactyloidites jordii* isp. nov. that are orientated perpendicular to bedding showing the typical “n”-shaped burrow cross section. Scale bar: 1 cm.

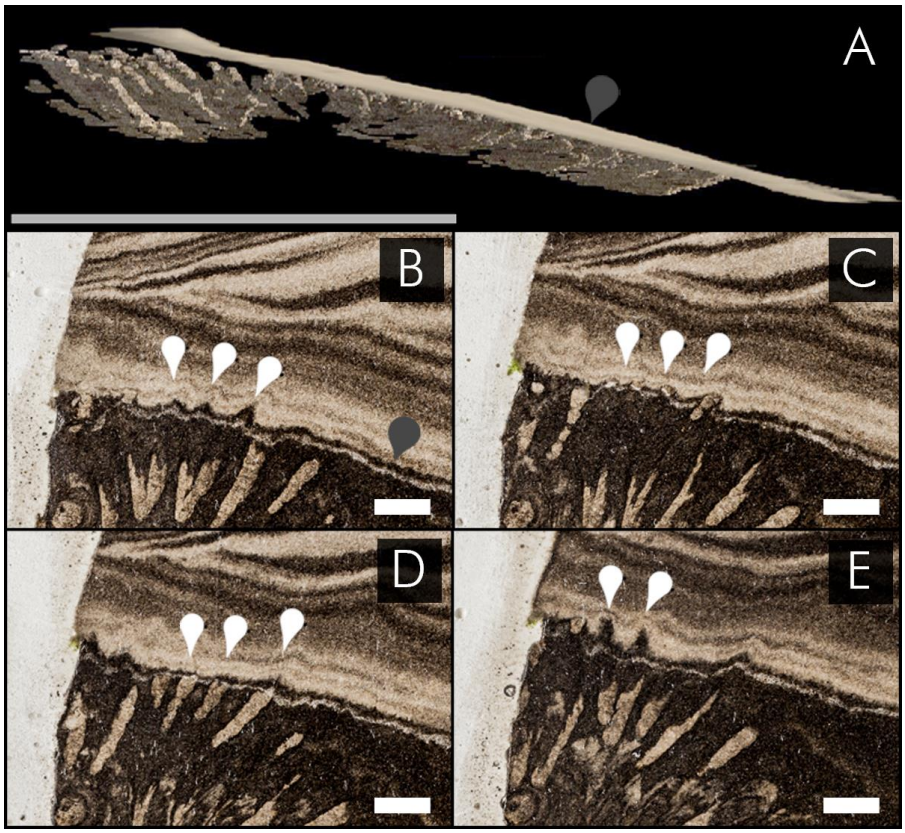

FIGURE 5. The effect of sediment heterogeneity on burrow morphology in *Dactyloidites jordii* isp. nov. A) three-dimensional view of the erosional surface against which *D. jordii* abuts; B-E) Sequential images 0.6mm apart that show the erosional contact (dark grey icon) within the sample (A) and overlying sediment that clearly pre-dates the burrow since the erosional surface is affected by the underlying *Dactyloidites*. Scale bars: 10 cm (A), 1 cm (B-E).

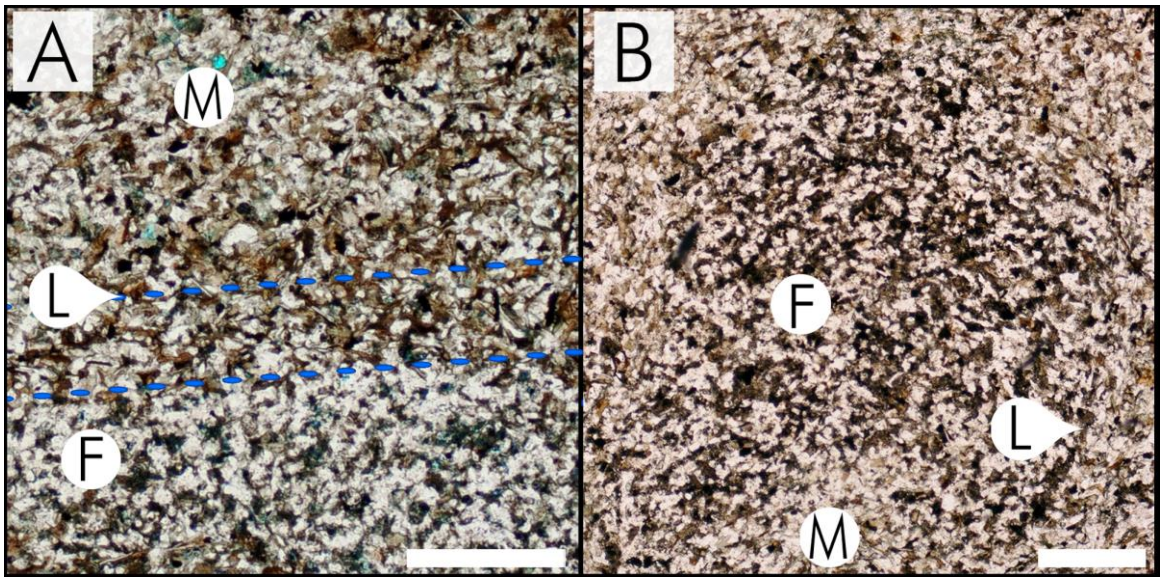

FIGURE 6. Thin sections of a radiating branch of *Dactyloidites jordii* in plane polarized light. A) Longitudinal section showing the grain orientation in burrow lining, and the cleaner sandstone of the burrow fill; B) Transverse cross section showing the typical n-shaped burrow cross section. M indicates the matrix, L points to the burrow lining, F indicates the burrow fill. Scale bar: 1 mm.

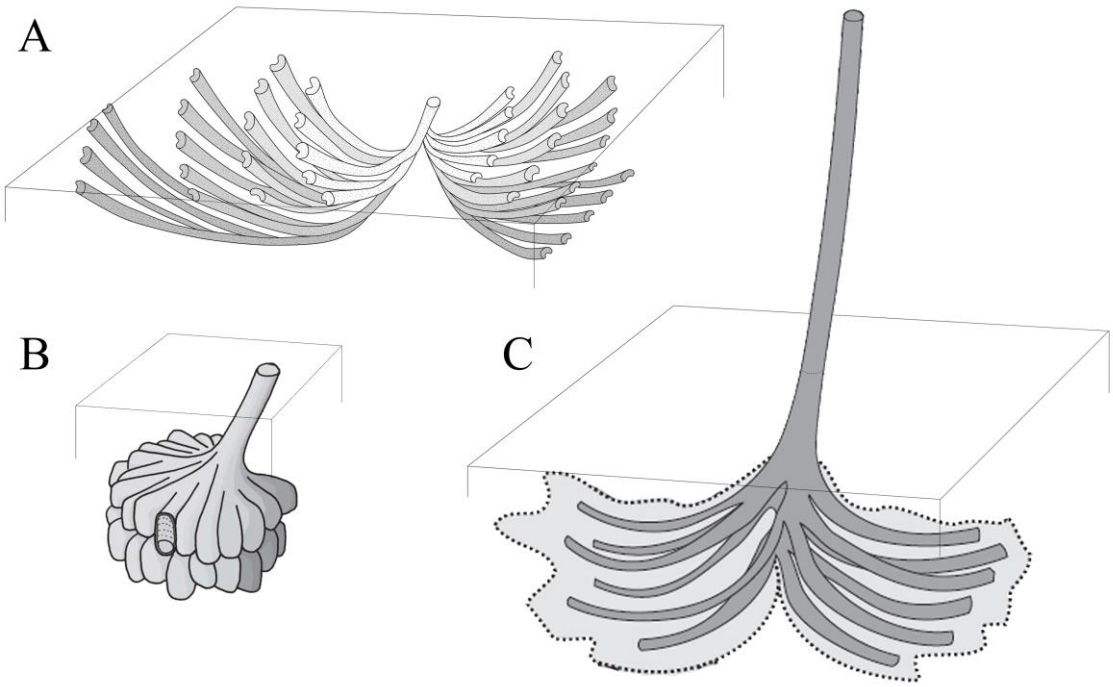

FIGURE 7. Line drawing comparison of *Dactyloidites jordii* (A), *D. ottoi* (B), and *D. peniculus* (C). Images are drafted to relative scale. B is redrafted from Gilbert et al., 2007 (redrafting from Fürsich and Bromley, 1985); C is redrafted from Uchman and Pervesler, 2007.

4. Palaeobiology

The tracemaker of *Dactyloidites ottoi* is widely considered to be an organism analogous to the modern polychaete *Arenicola marina* (Fürsich and Bromley, 1985; Wilmsen and Niebuhr, 2013). The feeding behaviour of *A. marina* in nutrient-dense sediment involves bulk sediment deposit-feeding from a stable shaft position to produce a series of radiating burrows (Rijken 1979) in a manner similar to that proposed for *D. ottoi* (Bromley, 1990, 1996; Wilmsen and Niebuhr, 2013). We note that the original observations of Rijken would result in longer, narrower radiating limbs, with more

frequent branching than in *D. ottoi* (though similar to our *D. jordii*). The redrafting of Rjiken's diagram by both Bromley (1990, 1996) and Wilmsen and Niebuhr (2013) includes modifications to create the impression that *Arenicola* produces shorter, broader limbs without branching, and thereby more closely resembling *D. ottoi.* It is unclear whether these changes are conceptual or based upon unpublished experimental observations.

The probing tubes of *D. jordii* extend outward through the sediment from its central shaft forming two broadly symmetrical rosette-shaped groups of burrows (Figs. 3, 7) that are generally arranged in galleries. The groups of radiating burrows display in excess of four orders of primary successive branching, and can branch both vertically and horizontally (Fig. 8). The radial burrows are considered to have been open structures that, based on the presence of a prominent lining that may have conferred stability to the burrow, were maintained for a period of time before being progressively filled with clean sand. Prior to being filled, the burrows bifurcate, possibly providing the source of clean sediment to fill the previous branch. *Dactyloidites* is concentrated in areas of the sediment with higher concentrations of organic detritus, high clay content, and are observed in one case to terminate at an inclined erosional surface that is overlain with clean sandstone poor in organic-matter (Fig. 5).

The burrowing strategy of *D. jordii* involves forming the deepest probe first, with each subsequent subhorizontal to upwardly inclined set of branches developing proximal to the previous branch (Fig. 9). As sediment was excavated for each new probe, a relatively thick burrow lining is constructed which was continuous along the complete

length of all burrows. Removed sediment was processed and likely packed in previous open probes, or deposited at the sediment-water interface. After completing the first layer of radiating probes, the tracemaker is inferred to have produced branches at successively shallower depths in the sediment, repeating the subhorizontal radial branching stage to produce stacks of radiating burrows (Fig. 9). This ideal pattern of branching can be disrupted where the lateral branches encounter clean (organic-matter poor) sediment. Upon encountering clean sand overlying an erosional surface, the tracemaker of the reconstructed burrow terminated the normal development of the radial portion of the burrow, and created progressively deeper tiers of radiating burrows (cf. Figs. 5 and 9). The anomalous downward stacking of the sets of radiating burrows may be repeated several times from the outer portion of the previous shallower rosette (Fig. 9). All the successive deeper tiers of the burrows were found to extend to the erosional surface before repeating the pattern of downward branching to produce deeper tiers of *D. jordii* (Fig. 5). This hypidiomorphic burrow development demonstrates that the response of the trace-making organism to chemosensory or tactile stimuli that detect low organic matter content or texture is to terminate lateral branching and search deeper levels of the sediment for detrital food resources.

Transverse cross sections of the burrow are typically “n”-shaped. This morphology is considered to reflect the body design of the trace-making organism, potentially reflecting the ventral morphology of a vermiform organism, or the bilateral appendages of an arthropod. The fill of a single branch of *Dactyloidites* was determined from petrographic analysis to have higher porosity than that of the surrounding matrix

(6% versus 2–3%), and the burrow lining was found to have a porosity of less than 1% (see supplementary materials). The clay-rich, low-porosity burrow lining may have served as a form of protection from either predation and/or adverse porewater conditions (cf. Kristensen and Kostka, 2005).

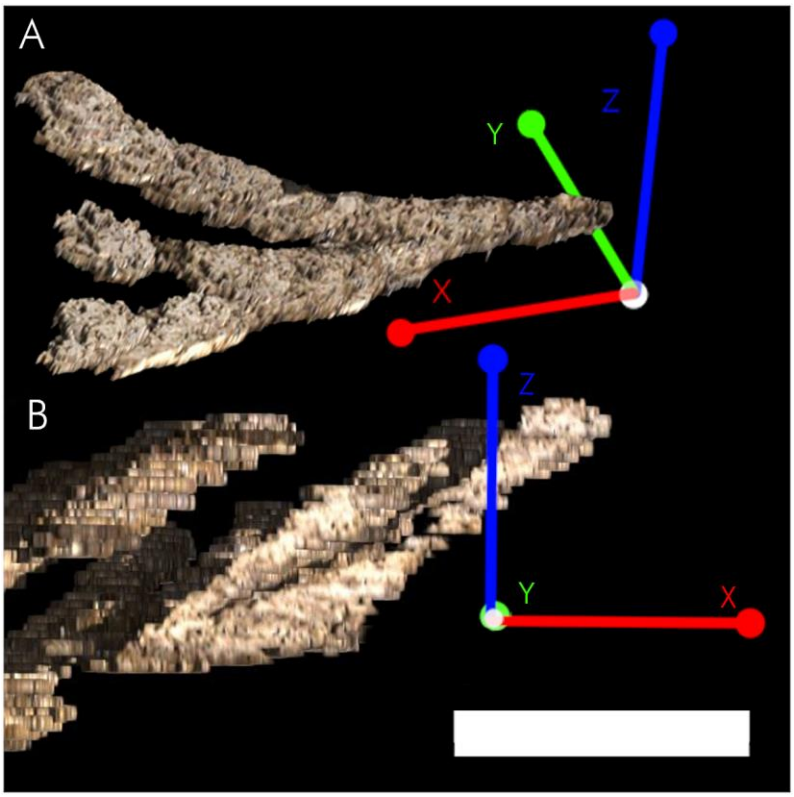

FIGURE 8. Primary successive branching as observed in both horizontal (A) and vertical (B) cross sections of *Dactyloidites jordii* displaying horizontal (A) and vertical (B) branching. Bedding plane is the X-Y plane. Serial grinding was performed along the Z axis. Scale bar: 1 cm.

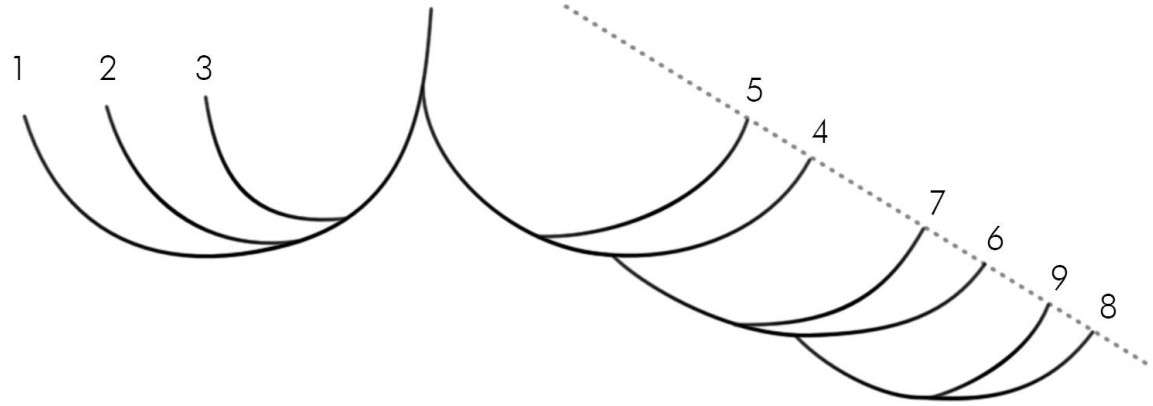

FIGURE 9. Hypidiomorphic burrow construction observed in sections A (left) and B (right) of *Dactyloidites jordii* burrow as it terminates against an erosional surface overlain by clean sandstone (demarcated by the dotted line). In probes 1-5 the idiomorphic pattern of branching is upheld. Where there is insufficient space to allow a more proximal burrow to probe 5, the burrowing program is altered to produce a deeper tier burrow (probes 6-7), which are in turn followed by an even deeper tier (probes 8 and 9). These deviations from the idiomorphic burrow pattern produces the hypidiomorphic morphology of the reconstructed specimen in the type series.

5. Conclusion

Five ichnospecies of *Dactyloidites* are currently valid; *D. asteroides* Fitch 1850 (the type ichnospecies), *D. cabanasi* Meléndez in Cabanás, 1966, *D. ottoi* Geinitz 1849, *D. peniculus* D'Alessandro and Bromley 1986, and *D. jordii* isp. nov. described herein. *Dactyloidites jordii* differs from the other ichnospecies of *Dactyloidites* in having numerous clay-lined radiating burrows with multiple orders of primary successive branching. These burrows are typically narrower than those of any other ichnospecies, are much longer than those of *D. ottoi*, and do not have the self-crossing and tight

overlapping clusters of *D. peniculus* (Fig. 7). As the rays of the Cambrian ichnospecies, *D. asteroides* Fitch (1850) and *D. cabanasi* Meléndez in Cabanás (1966) are broad, and do not display any branching, they are considered to differ significantly from *D. jordii;* as such we do not directly compare these ichnospecies herein. Re-examination of the type material for both ichnospecies is recommended.

The complex three-dimensional morphology of *Dactyloidites jordii* is inferred to be the result of a marine invertebrate sequentially excavating burrow probes in search of organic material. The probes were created as open structures supported by a constructed burrowing lining prior to being actively filled with the organic matter and clay-poor sediment derived from the newly opened adjacent burrow probe. The *D. jordii* making organism systematically created tiers of both horizontally and vertically branched probes. The idiomorphic burrow morphology is such that the deepest probe was created first and shallower probes were created subsequently. It is suggested that trace-making organism could alter its search pattern upon encountering non-ideal conditions (cf. Figs. 5 and 9). The adaptive nature of trace making organisms highlights the need for ichnologists to provide a type series rather than a single holotype, in order to capture the inherent range of possible burrow morphologies.

Acknowledgements

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CHAPTER THREE

Three-dimensional morphology of *Beaconites capronus* from Northeast England

(Accepted manuscript with Ichnos)

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KEYWORDS

Beaconites; Serial Grinding; Three-Dimensional Reconstruction; Ichnology; Ichnotaxonomy; Stainmore Formation

*This chapter is formatted according to the standards set by *Ichnos*

ABSTRACT

Beaconites capronus is a winding, meniscate, backfilled trace fossil differentiated from comparable ichnotaxa *Taenidium* and *Ancorichnus* on the basis of its distinct and unornamented burrow lining. Typically horizontal to sub-horizontal *B. capronus* also includes vertical pipes which serve as a point of entry for endobenthic deposit feeding activity. The burrows do not self-cross but often display secondary successive branching potentially indicating coprophagous feeding strategies in lower nutrient sediment. *Beaconites capronus* material is examined and discussed from the Carboniferous offshore transition zone deposits near Howick, United-Kingdom. Samples were collected and analysed using high-resolution serial grinding and modelling techniques documenting fine detail in three dimensions. As the burrows were actively backfilled and did not maintain a connection to the sediment-water interface, the tracemaking organism must have had a method of coping with low oxygen porewater conditions. Three methods are considered herein 1) revisiting the sediment-water interface, 2) creating periodic shafts, or 3) employing the use of obligate anaerobic metabolism. Based on the material presented herein, an emended ichnospecific diagnosis is provided.

INTRODUCTION

The type material of the lined, backfilled, meniscate winding trace fossil was originally described from shoreface through offshore deposits of Carbon County, Utah. *Beaconites capronus* is distinguished from all other ichnospecies of *Beaconites* Vialov by the distinctive chevron-shaped cross-section of its backfill. The primary ichnotaxobase used to differentiate among meniscate ichnogenera is the presence or absence of a burrow lining (Keighley and Pickerill, 1994). The ichnogenus *Beaconites* encapsulates all meniscate trace fossils with a pronounced burrow lining (Keighley and Pickerill, 1994). Meniscate traces that are thinly lined or unlined burrows are classified under the ichnogenus *Taenidium* Heer, and those with an outer mantle (i.e., an outer zone of burrow fill; *sensu* Keighley and Pickerill, 1994) belong to *Ancorichnus* Heinberg. *Beaconites* was created as a monotypic ichnogenus, containing only the ichnospecies *B. antarcticus*. Although the original diagnosis of *Beaconites* did not mention the presence of a lining (Vialov, 1962), its presence has been suggested by examination of topotypes (Bradshaw, 1981). The ichnogeneric diagnosis was therefore subsequently emended to include the presence of a distinct, smooth and unornamented burrow lining (Keighley and Pickerill, 1994). Upon examination of additional *B. antarcticus* material the prominence of the burrow lining described by Bradshaw, and its significance in differentiating it from the lining associated with *Taenidium* was questioned (Goldring and Pollard, 1995; Retallack, 2001). Although the taxonomic status of *Beaconites* has been discussed, it has never been deemed a nomen nudum, nomen dubium, nomen oblitum, or otherwise invalidated and is in continued use throughout the literature. According to the International Commission for

Zoological Nomenclature (2010) the designation of a type species is purely for nomenclatural purposes, and a type species need not to best typify the genus. As such, regardless of the status of *B. antarcticus*, we consider that the name *Beaconites* is useful to describe meniscate traces with a pronounced lining, and are of the opinion that it should remain in use.

For this study, samples of exceptionally well-preserved *Beaconites capronus* were collected from heterolithic sandstone and siltstone beds of the Carboniferous Stainmore Formation, which outcrops near Howick in the United Kingdom (Fig 1). These samples were processed using the serial grinding and reconstruction methods described in Bednarz et al. (2015) to produce high-resolution three-dimensional models that were used to investigate the burrow morphology of *Beaconites capronus* and its interactions with the near-burrow environment.

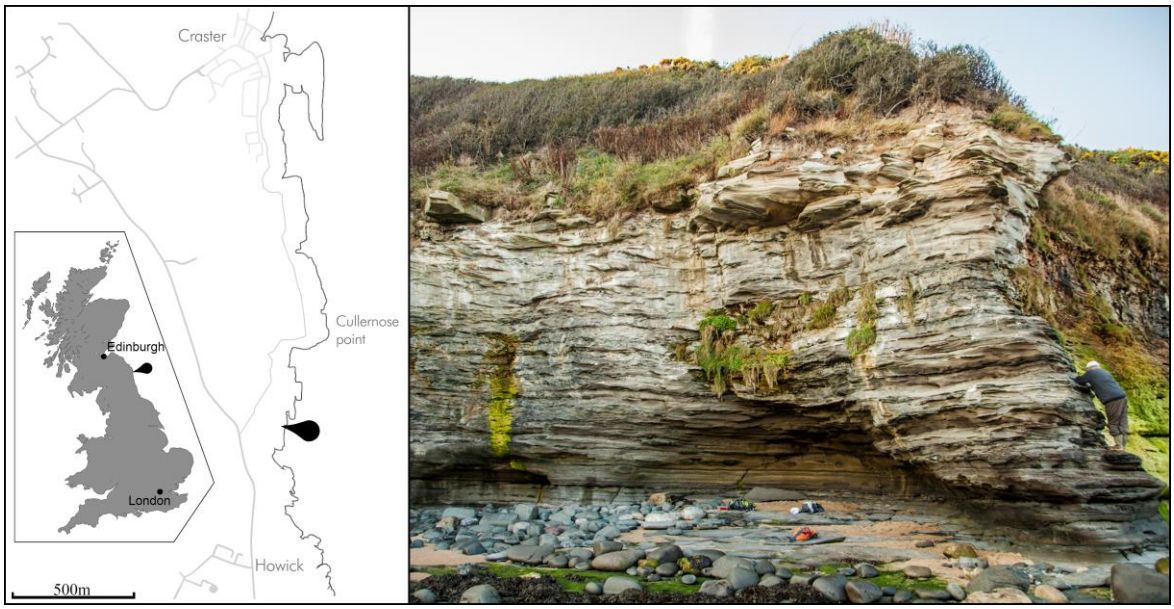

Figure 1. Black icon indicates location of field work between the towns of Howick and Craster, United Kingdom. The Carboniferous interbedded sandstone and siltstone beds of the Stainmore Formation are inferred to have been deposited in a storm-dominated marine setting, below the fair weather base but above the storm wave base.

GEOLOGIC SETTING

The samples for this study were collected from the Carboniferous (late Mississippian/early Pennsylvanian) Stainmore Formation of the Yoredale Group in a small cove between the towns of Howick and Craster, Northumberland, United Kingdom (Fig 1; N 55° 27′30.38″, W 1° 35′34.32″). The succession is composed of centimetre to decimetre scale interbedded siltstone and sandstone forming upward-coarsening parasequences. The inter-beds are composed of alternating clean sandstone and clay/mica rich siltstones rich in illite, muscovite, biotite, and chlorite/serpentine of both detrital and diagenetic origins. The thickest sandstone beds show evidence of high-energy wave

reworking including hummocky cross stratification. The interbedded clean sandstones and clay rich siltstones are considered to have been deposited in storm-dominated offshore environments around the offshore transition zone.

METHODOLOGY AND MODELLING

The methodology employed for this study follows that of Bednarz et al. (2015). The samples studied were from closely localized float material that was encased in plaster and serially ground using a CNC milling machine with a diamond-carbide cutting tool. The grind interval for this study consisted of 0.3 mm increments. After each successive surface was ground, the samples were wetted with oil and photographed. The photographs were then image-processed to create consistent exposure and colour corrections. The stack of corrected images was subsequently imported into Adobe Photoshop where each image was aligned and burrows were digitally extracted from the overall image. This series of extracted selections were then modelled in the volume graphics software VG Studio Max. Modelling the burrows in this way allows for digital sectioning in any plane and study of the specimen from any angle (Fig 2). More than 15 *Beaconites* were modelled for this study, some of which were only partially preserved. The precise morphology of some burrows was difficult to visualize because of their high density. To aid in interpretation, a single well-preserved burrow was selected and modelled separately to best visualize its component parts (Fig 2B). In addition to modelling the burrow selections, the complete succession of rock images were examined producing a model of

the full sample comparable to a CT scan image array (Fig 2A). The whole-sample model allows for visualization of the burrows in relation to one another and in the context of the sediment surrounding the burrow, the latter being a significant advantage to palaeobiological interpretation.

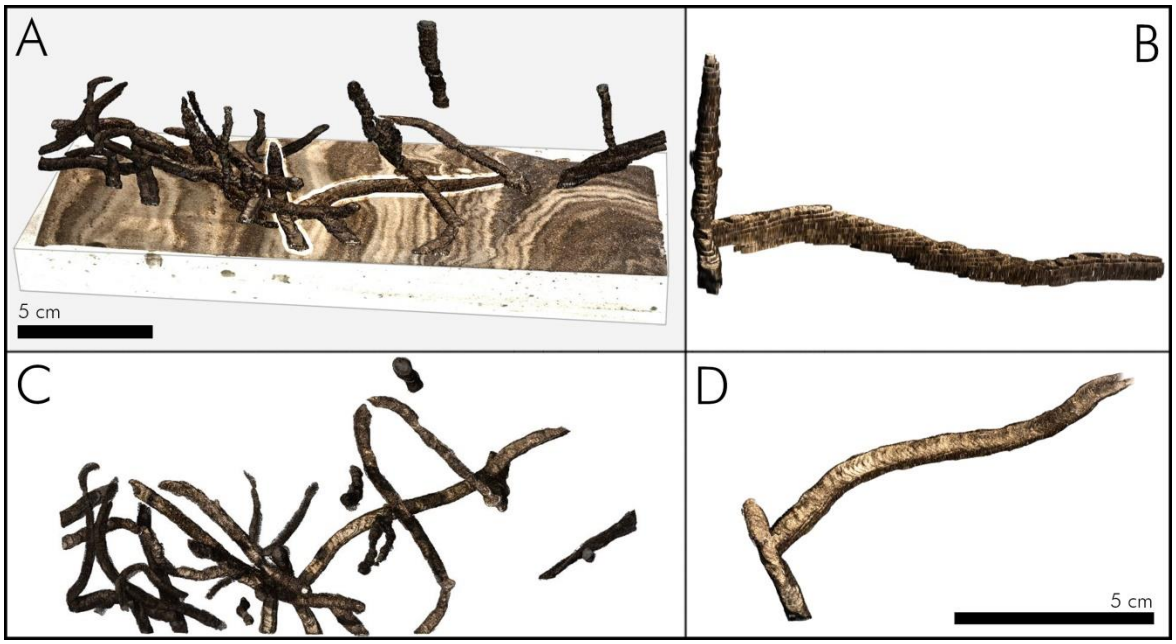

Figure 2. A) *Beaconites capronus* fabric illustrating complex association of various burrows, which do not self-cross. Burrows are typically horizontal to sub-horizontal with vertical shafts being associated with some specimens. B) Isolated *B. capronus* burrow (highlighted in A) display connection between vertical pipe and the sub-horizontal portion which displays secondary successive branching (bedding-perpendicular view); C) *Beaconites capronus* fabric viewed from above (bedding-parallel) demonstrating burrow density and sinuosity; D) Highlighted burrow in A sectioned to show chevron-like meniscate backfill in horizontal cross section.

RESULTS

BURROW MORPHOLOGY

Approximately fifteen burrows belonging to *Beaconites capronus* were modelled, of which only four are longer than a couple of centimetres in length. The remaining burrow fragments are truncated by the edges of the sample or by an erosive boundary within the sample, or else are discontinuous within the sample. The burrows display a range of morphologies including distinct vertical, subvertical, and horizontal components. Nevertheless, the burrow dimensions are relatively consistent, being on average approximately 7 mm in diameter, and with a burrow lining that is 0.5-1.2 mm thick. The burrows are composed of alternating silt-rich and clay-rich mudstone menisci that have approximate thicknesses of 1 mm and 0.5 mm respectively. The backfill is arranged in a blunt chevron as seen in cross section (Fig 3), which is diagnostic of *Beaconites capronus* (Keighley and Pickerill, 1994). The average chevron angle is around 90°, with a corner radius between 0.5 and 1 mm (Fig 3). The overall ratio of clay to siltstone in the burrow fill ranges greatly (Fig 4). The ratio of clay-rich to silt-rich menisci is not considered to reflect ethological differences so much as grainsize differences in the host sediment as the trace-maker passed through the stratified, heterolithic beds. Changes in mineralogy of the burrow fill commonly occur along the length of a single burrow in response to heterogeneity of the burrowed sediment rather than being controlled by the tracemaking organism (Fig 4B).

While *Beaconites capronus* is generally a predominantly horizontal burrow, several vertical burrows with *B. capronus*-like wall and fill have been found to be continuous with the sinuous, horizontal segments of the burrow (Fig 2). The vertical segments preserved in this sample are at least 2.4 cm long, but their complete length is unknown as they cut the upper surface of the sample. Vertical pipes longer than 5 cm were observed in the field (Fig 5), and broadly resemble the subvertical components of the trace fossils *Siphonichnus* or *Schaubcylindrichnus heberti* (cf. Evans and McIlroy, 2016). The vertical segments of *B. capronus* show a gradual change in orientation where they are continuous with the more familiar horizontal burrows. The burrow lining thickness and shape of the meniscate backfill of the vertical components of *B. capronus* are identical to those of the horizontal portions of the burrow (Fig 6). The only difference between the horizontal and vertical components is that the cross-sections of vertical burrows are circular, while those of horizontal burrows are oval. This is considered to be the result of burial compaction that causes the *B. capronus* in transverse section to have cross sections that are approximately twice as wide as they are high.

The original diagnosis of *Beaconites* (*Ancorichnus*) *capronus* stated that it is rarely branched (Howard and Frey, 1984), but the rare presence of branching was omitted from the emended diagnosis of *Beaconites capronus* by Keighley and Pickerill (1994). Although the removal of rare branching as a diagnostic character was not discussed, it may be that the rare branching noted by Howard and Frey (1984) was considered to be false branching or secondary successive branching by Keighley and Pickerill (1994). No true branching has been observed in our material, in all cases of apparent branching,

secondary successive branching can be demonstrated (Fig 7). This suggests that secondary successive branching, which is the result of an organism reworking a pre-existing burrow before diverging from it (D'Alessandro and Bromley, 1987), was common behaviour of the *B. capronus* trace-maker in these strata, and additionally no evidence has been observed indicating reworking by the same organism. The two most likely reasons for re-burrowing a pre-existing burrow are: 1) the trace-making organism re-burrowed an earlier burrow to exploit microbial growth on faecal material or mucus deposited by an earlier trace maker (coprophagy); or 2) in well compacted sands less energy may have been required for re-burrowing a burrow than excavating the host sediment. The burrows observed in this study do not self-cross, though the sample is comparatively small, suggesting that if the purpose of re-burrowing is coprophagy, then the behaviour is allocoprophagy. The burrows in this sample are all sinuous in plan view, with some showing relatively tight meander-like loops where the corner radius is on average equal to the burrow diameter (Fig 8). These burrows are commonly cut by later burrows in the ichnofabric, primarily *Dactyloidites* isp., which *B. capronus* never crosscuts, suggesting that these *Beaconites* represent early colonization of the substrate by adult immigration (cf. McIlroy, 2004).

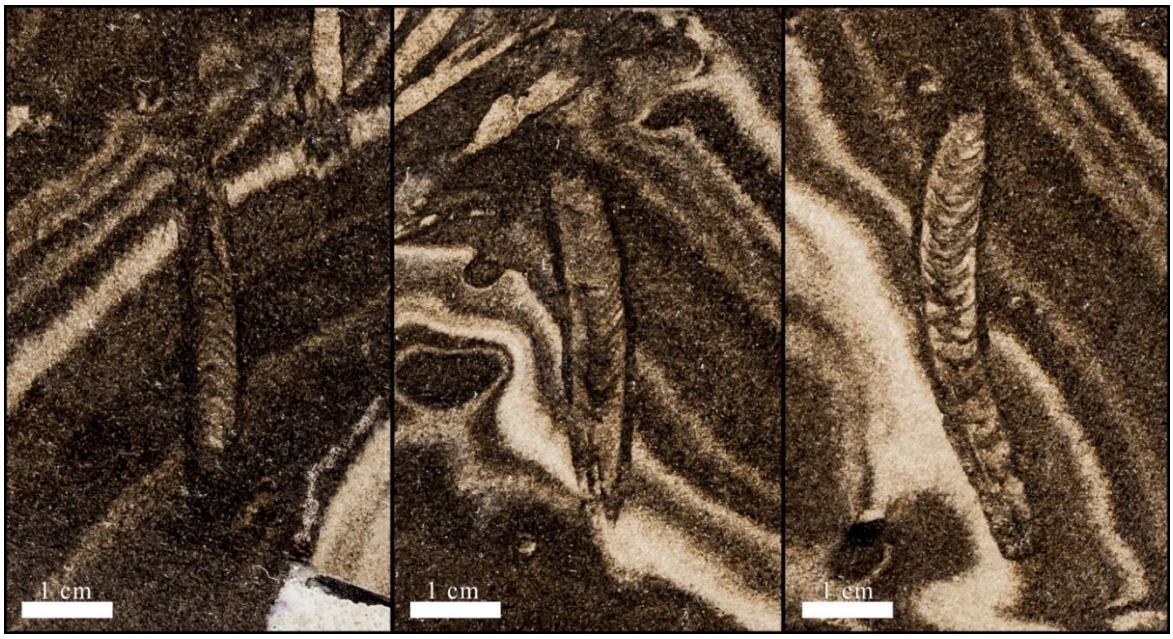

Figure 3. Three *Beaconites capronus* longitudinal-sections showing the diagnostic chevron-shaped backfill.

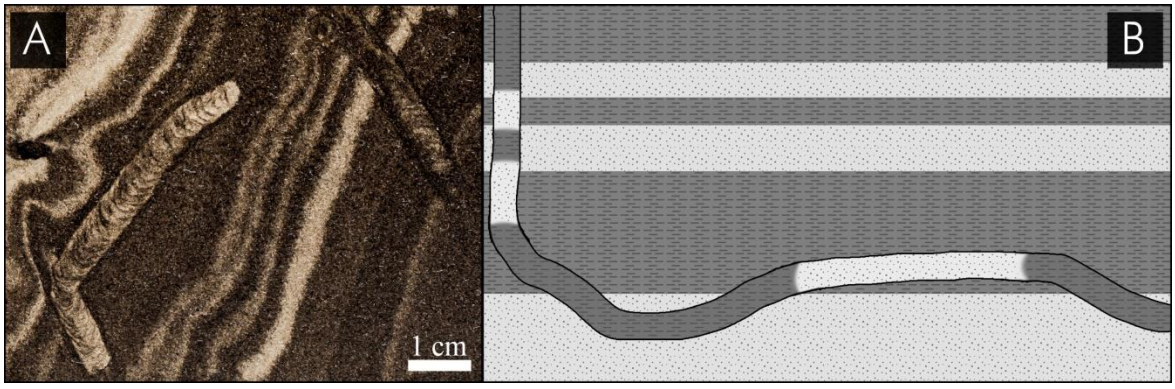

Figure 4. A) Variation in fill composition of two burrows belonging to *Beaconites capronus*; B) Model for variation in fill composition resulting from a lag between the points of ingestion and egestion (redrafted from Seilacher, 2007).

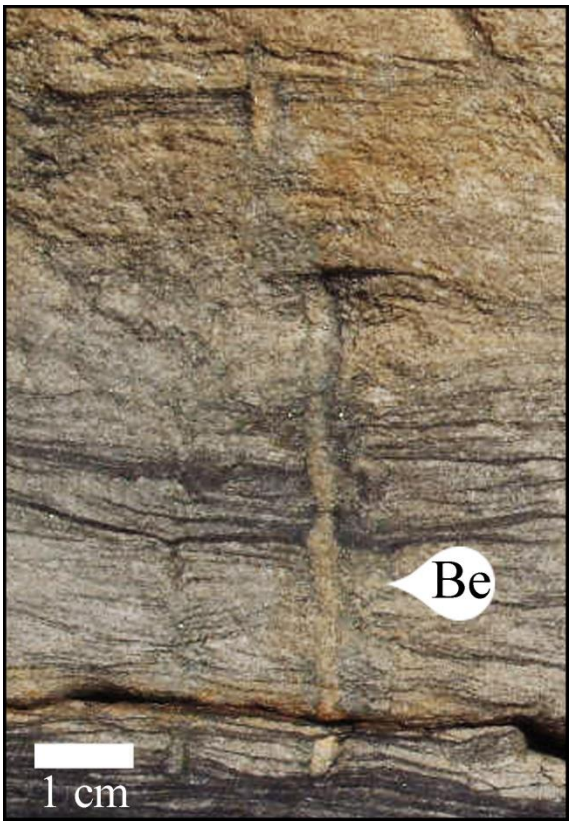

Figure 5. Vertical pipes of *Beaconites capronus* (Be) in the field.

Figure 6. Vertical portion of *Beaconites capronus* burrow with lining and meniscate backfill.

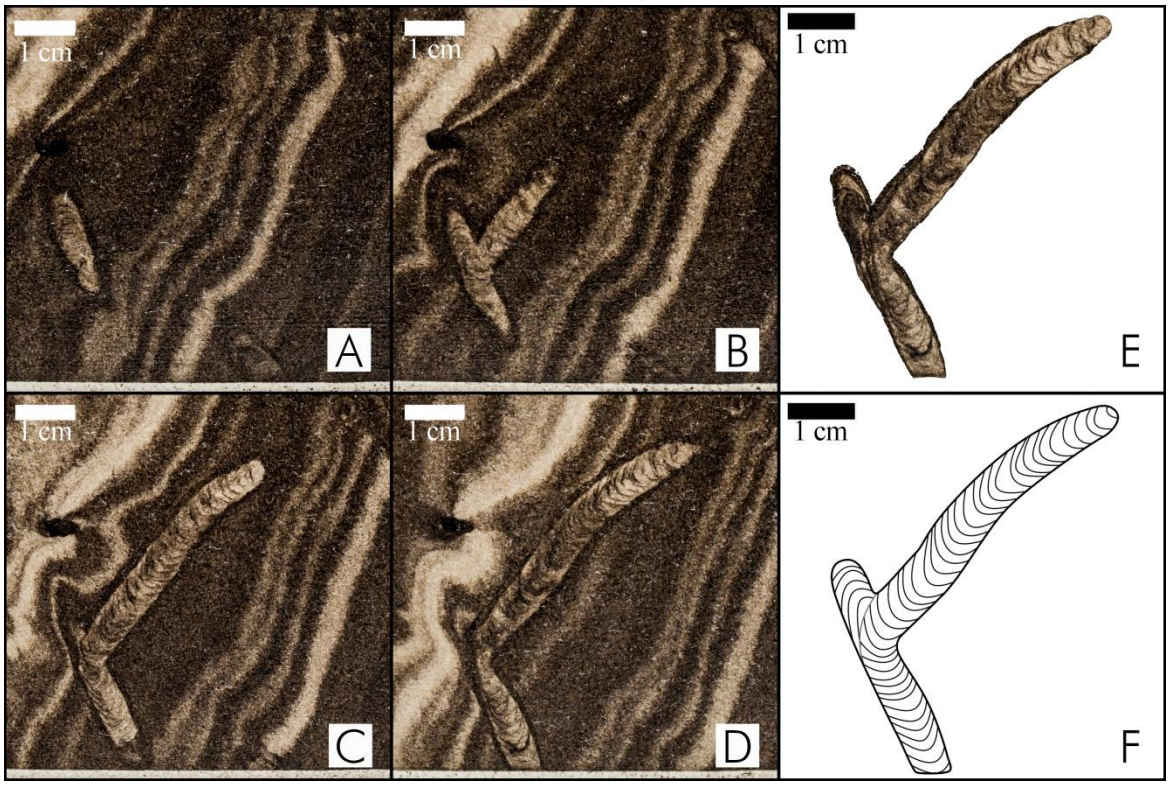

Figure 7. Secondary successive branching shown in *Beaconites capronus*. Images A-D are sequential images taken 0.6 mm apart: E) Composite cross section image generated from stacked serial ground images; F) Draft showing the orientation of menisci.

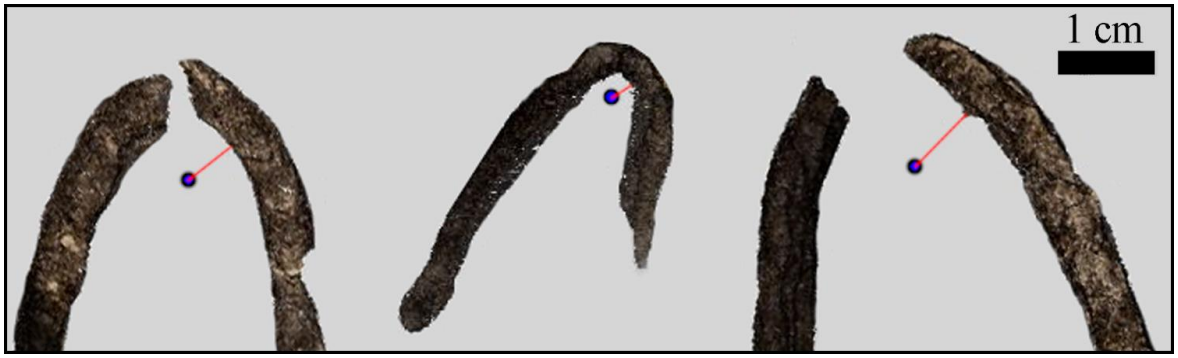

Figure 8. Turning angle/corner radius for three *Beaconites capronus*. Gaps in A and D are from cross cutting relationship with *Dactyloidites isp.*

SYSTEMATIC ICHNOLOGY

The ichnogenus *Beaconites* was introduced in 1962 by monotypy (*B. antarcticus)* for material from a sandstone unit at Beacon heights in Antarctica (Vialov, 1962). No type specimen was collected, the rock slabs of the uncollected type material are highly weathered, and the description of the type material was lacking in detail (Vialov, 1962). The taxonomic status of *Beaconites* has thus been controversial (Gevers et al., 1971; Bradshaw, 1981), but was somewhat stabilized by the emended diagnosis of Keighley and Pickerill (1994), who restricted *Beaconites* to meniscate burrows with "distinct, smooth and unornamented burrow linings" (Fig 9). The presence of a burrow lining in the type species of *Beaconites* (*B. antarcticus*)—the basis upon which *Beaconites* can be distinguished from *Taenidium*—has been discussed by several authors, who questioned the validity of *Beaconites* (Goldring and Pollard, 1995; Retallack, 2001). Regardless of the status of *Beaconites antarcticus*, we preserve *Beaconites* as a useful name taxonomically and maintain that it should be used on the grounds of nomenclatural stability for meniscate traces as per the emended diagnosis provided by Keighley and Pickerill (1994). Maintaining ichnotaxa on the basis of emended diagnoses for nomenclatural stability has been previously applied to *Planolites* Nicholson and *Palaeophycus* Hall. Although *Planolites* was strictly speaking a junior synonym of *Paleophycus*, both names were maintained on the basis of its emended diagnosis (Keighley and Pickerill, 1995).

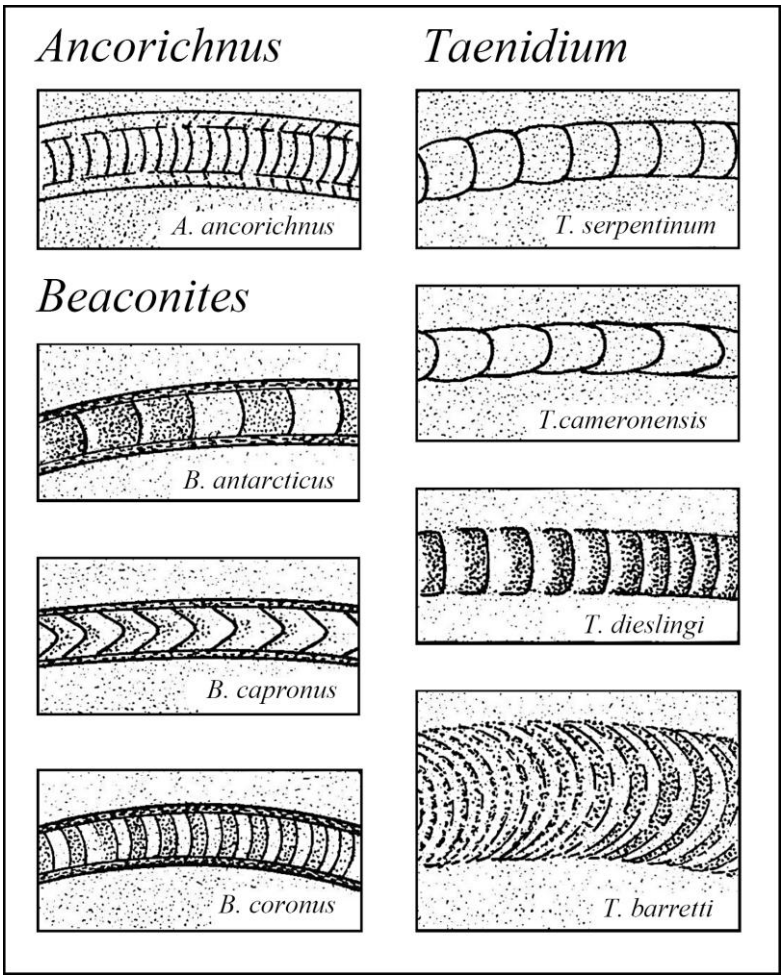

Figure 9 – Diagrammatic representation of the differences between *Ancorichnus*, *Beaconites*, and *Taenidium*, from Keighley and Pickerill, 1994.

Ichnogenus ***Beaconites*** Vialov, 1962

Type ichnospecies: *Beaconites antarcticus* Vialov, 1962 (by monotypy).

Diagnosis: Small, cylindrical, walled, meniscate burrow occasionally exhibiting secondary successive branching. Burrows are straight or sinuous, horizontal or more rarely inclined or vertical. Burrows consist of weakly to strongly arcuate meniscate

packets or segments enclosed by distinct, smooth and unornamented burrow linings (after Keighley and Pickerill, 1994).

***Remarks*:** The presence and prominence of a burrow lining is the key feature that distinguishes *Beaconites* from other meniscate traces (Keighley and Pickerill, 1994). *Beaconites* was distinguished as a monotypic ichnogenus with no mention of the presence or absence of a burrow lining, and with only one field photograph serving as the type material (Vialov, 1962). Examination of topotypes allowed a diagnosis to be created for *B. antarcticus* that mentioned a poorly developed sand lining (Bradshaw, 1981). The presence of a burrow lining was later used as the differentiating characteristic that separated *Beaconites* from comparable meniscate traces, *Taenidium* and *Ancorichnus* (Keighley and Pickerill, 1994). Although the radiating limbs of *Phoebichnus* are comparably lined with meniscate filled tubes, the burrow structure as a whole is distinctly stellate (Evans and McIlroy, 2015). The taxonomic status of *Beaconites* has been questioned on the basis that the lining described for *B. antarcticus* is insufficient to differentiate it from the ichnogenus *Taenidium* (Goldring and Pollard, 1995; Retallack, 2001). As *Beaconites* has not been formally invalidated and the fixation of a type species is for purely nomenclatural purposes, and not on the basis of which species best typifies the genus, we consider *Beaconites* a valid and useful name in differentiating meniscate traces and recommend its continued use.

Beaconites capronus Howard and Frey, 1984

Emended diagnosis: Predominantly horizontal to subhorizontal, straight to sinuous, lined cylindrical burrows with chevron-shaped, meniscate backfill. Burrows typically does not self-cross and does not display true branching, but occasionally exhibits secondary successive branching. Rare vertical pipes with identical lining and meniscate fill may be present.

***Remarks*:** The type material of *Beaconites capronus*, which was in the possession of Robert W. Frey, has been misplaced following his passing (Andrew Rindsberg, pers. comm., 2015). It is recommended that the Panther Member of the Star Point Formation of the Cordingly Canyon, near Price, Utah (the type locality) be revisited and sampled and a neotype be fixed in its absence. *Beaconites capronus* is differentiated from *B. coronus* by the distinct chevron shape of the meniscate fill. *Beaconites antarcticus* is differentiated from *B. capronus* and *B. coronus* by having larger and typically heterogeneous packets composing the burrow fill.

DISCUSSION

Palaeobiology

The maker of *Beaconites capronus* remains unknown as no body fossil of a potential tracemaker has been discovered within these burrows. Modern meniscate burrows are produced by a wide range of organisms including molluscs (bivalves or gastropods), arthropods, larval insects, soft-bodied worm-like organisms, and some

vertebrates (e.g., Howard 1966; Frey et al., 1984; Mángano et al., 1998; Counts and Hasiotis, 2009; Melchor et al., 2012; Neto de Carvalho et al., 2015). The morphology of the burrow does, however, provide some evidence for both the trace-maker body plan and the mechanics involved in the production of *B. capronus*. From this information inferences can be made about trace-maker ethology. The meniscate back-fill and the vertical shafts that descend into the sediment and pass through an erosive surface demonstrate that the organism was moving endobenthically. The generally broad meandering pattern, wide turning radius, and few relatively tight bends of the burrows suggests a long but flexible body design (Fig 8). The circular burrow cross section indicates that the trace-maker likely had an axially circular body. This line of evidence is consistent with a vermiform trace-maker.

Nutrition

Meniscate backfill of burrows similar to *Beaconites* in marine environments is often interpreted as being the result of endobenthic deposit-feeding behaviour (e.g., Howard and Frey, 1984; Plaziat and Mahmoudi, 1988; Bromley, 1996; Mángano et al., 1998). These menisci have been interpreted as the result of grain-selective deposit-feeding behaviour of the trace-making organism in which grains of suitable size and food quality are ingested and passed through the organism, whereas rejected or sorted material is passed around the body (Clifton and Thompson, 1978; Keighley and Pickerill, 1994; Bromley, 1996). This kind of feeding behaviour can lead to large amounts of both

ingested and rejected material being packed behind the organism as meniscate backfill (Bromley, 1996; Counts and Hasiotis, 2009; Brasier et al., 2013).

The presence of a burrow lining is also suggestive of selective feeding, as some materials are passed around the organism, rather than exclusively passing through its gut. As burrowing organisms force their way through the sediment during sediment processing, internal pressures within the open portion of the burrow are increased, which can force water out of the burrow and cause clay-grade material to become trapped against the burrow wall, forming a semiconsolidated burrow lining (Jumars et al., 2015). Additionally, the burrowing organism is likely to have secreted a mucous burrow lining that may have aided in the adherence of clay grains to the burrow walls as rejected sediment passed backward during burrowing.

Burrowers may selectively digest particles based on various physical traits such as grain size, roughness, and specific gravity (Clifton and Thompson, 1978; Self and Jumars, 1978, 1988; Bednarz and McIlroy, 2012). Grains are also potentially selected based on various organic criteria such as the presence or absence of a bacterial or organic grain coating (Taghon, 1982; Guieb et al., 2004). Whether the grain-selection process during feeding was sensory or mechanical, it is highly unlikely that it was a perfectly efficient process (cf. Jumars et al., 2015). Bulk-sediment deposit feeding organisms characteristically have low gut residence times and need to ingest large amounts of sediment to gain sufficient nutrients (Kemp, 1986). All these suggest that the *Beaconites capronus* tracemaker was likely a microphagous, vermiform deposit-feeder that processed large amounts of sediment.

Newly backfilled meniscate packages likely contained both faecal and non-faecal elements with some nutrient content (Keighley and Pickerill, 1994). Over time this material may have stimulated additional microbial biomass, which would encourage ingestion of the meniscate backfill. The increase in labile organic matter content may have encouraged the trace maker to return to its own faecal matter (autocoprophagy) or exploit the pre-existing burrow fill of other organisms (allocoprophagy), which might lead to the secondary successive branching observed in the present material of *Beaconites capronus* (Fig 7).

Locomotion

The meniscate backfill present in *B. capronus* is also potentially related to locomotory processes. Some organisms burrow within sediment by relocating material that is excavated from in front of the organism and packing it behind during forward movement (Chamberlain, 1971; Kanazawa, 1992; Keighley and Pickerill, 1994; Bromley, 1996; Fu and Werner, 2000; Gingras et al., 2008). Alternative or additional burrowing processes include self-anchoring via localized body swelling (cf. Truman, 1968), crack propagation (Dorgan et al., 2005), or by propulsion via setae or parapodia (Dorgan et al., 2006).

Vertical shafts

Vertical, cylindrical shafts are demonstrably connected to the bedding-parallel portions of the *Beaconites capronus* examined in this study (Fig 2). The vertical pipes are meniscate backfilled in a manner identical with that of the horizontal portion of the burrows into which they turn. As the menisci are oriented convex up, and therefore indicate a downward direction of movement they are interpreted as the point of entry of the trace-making organism into the sediment. The vertical shafts are in excess of five centimetres and, since they are continuously back-filled, demonstrate that trace-making organism did not maintain an open connection to the sediment-water interface. Since most seafloor sediments experience rapid decrease in pore-water oxygenation after burial (Precht et al., 2004), and since there was no connectivity between the burrow and the overlying seawater, it is likely that the tracemaker experienced significant oxygen stress. Coping with this porewater dysoxia can be approached by burrowing organisms in a number of ways: 1) revisiting the sediment-water interface; 2) creating periodic shafts (e.g., Bromley and Asgaard, 1975; Plaziat and Mahmoudi, 1988); or 3) employing the use of obligate anaerobic metabolism (cf. Danovaro et al., 2010; Mentel and Martin, 2010). At present too little work has been aimed at understanding the behavioural and metabolic approaches to surviving below the sediment-water interface in association with low oxygen pore-waters.

CONCLUSION

Beaconites capronus is a lined meniscate trace known from marine environments (Howard and Frey, 1984; Keighley and Pickerill, 1994). It is distinguished from other ichnospecies of *Beaconites* by its distinctively chevron-shaped backfill. The three-dimensional reconstructions created herein allow detailed investigation of the morphology of *B. capronus*, and facilitate palaeobiological consideration of the trace fossil. The *Beaconites capronus* trace maker was likely an endobenthic, microphagous, depositfeeding vermiform organism that may have engaged in coprophagous activity. The newly described vertical shafts and prevalence of secondary successive branching allow refinement of the ichnogeneric diagnosis of *Beaconites*. Secondary successive branching reflects the reworking of pre-existing burrows in order to exploit organic material contained within meniscate packages including mucus and faecal material by subsequent coprophagous burrowers. The presence of vertical shafts in *B. capronus* and the near-absence of burrows cross-cut by the trace, suggesting that the *B. capronus* trace-maker was probably a pioneer colonizer of rapidly deposited storm event beds, probably colonizing by adult immigration (cf. McIlroy, 2004). As a result of this study the diagnosis of *Beaconites capronus* is emended to incorporate the details observed herein.

ACKNOWLEDGEMENTS

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CHAPTER FOUR

Neoeione n. igen., and the morphology and method of formation of *N. moniliformis* from the Carboniferous of northern England.

(In review with the Journal of Paleontology)

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Keywords: *Neoeione; Eione; Parataenidium;* Serial grinding; three dimensional; ichnology

*This chapter is formatted according to the standards set by the *Journal of Paleontology*

ABSTRACT

Samples of the burrows studied herein, originally introduced as *Eione moniliformis* Tate, have been collected from the heterolithic sandstone and siltstone beds of a coastal outcrop near the town of Howick, Northumberland United Kingdom. These interbedded and hummocky cross stratified beds, belonging to the Stainmore Formation, are Carboniferous and represent offshore marine sediment deposited between fair wave base and storm wave base. As the name *Eione* was used previously to describe a genus of gastropod, *Eione* Tate is a junior homonym of *Eione* Rafinesque. Therefore, a new ichnogenus was established, *Parataenidium* Buckman, to accommodate burrows composed of two distinct levels and which included *E. moniliformis*. Using three-dimensional morphological modeling techniques, this study aims 1) to clarify the current taxonomic status of *Parataenidium moniliformis*, and 2) to provide an updated model for its construction via inferring the possible trace-maker ethology. The transfer of *Eione moniliformis* to *Parataenidium* was problematic; primarily because it is not composed of two distinct levels but instead composed of backfilled reniform sediment packages. These packages were created through a multistage process whereby the organism maintained a small open cavity from which it fed. Accordingly a new ichnogenus, *Neoeione*, is proposed to accommodate the material originally described by Tate.

Introduction

The material described herein was collected from coastal outcrops collected (coordinates 55° 27′30.38″ N, 1° 35′34.32″W) of the Stainmore Formation of the Upper Mississippian to Lower Pennsylvanian Yoredale Group (Dean et al., 2011; Fig. 1). The diverse ichnological assemblage of the Stainmore Formation includes burrows that Tate (1859) first introduced as *Eione*. The name *Eione* was subsequently discovered to be unavailable owing to its previous use for the gastropod *Eione* Rafinesque, 1814, which has led several authors to consider it as a junior homonym (Häntzschel, 1975; Rindsberg, 1994; Buckman, 2001), and led to its inclusion of Tate's *Eione moniliformis* within *Parataenidium* Buckman, 2001. *Parataenidium* (*Eione*) *moniliformis* has, to date, only been described from Carboniferous sediment. It has also been documented in the Salem Formation, which was heavily quarried and used extensively as a building stone in the eastern United States including in the construction of many famous buildings such as the empire state building and the pentagon (cf. Shrock, 1934). As such, many public buildings across the eastern United States exhibit *Parataenidium* (*Eione*) *moniliformis.*

Our field site is the locality from which Buckman (2001) collected the neotype of *Parataenidium* (*Eione*) *moniliformis* by Buckman, (2001). Given the close similarities among the lithology and morphology of our material, Tate's drawing, and the neotype (Fig. 2), we consider Howick to be the most probable type locality of *Parataenidium* (*Eione*) *moniliformis.* The Stainmore Formation consists of interbedded clay-rich siltstones and hummocky cross-stratified, clean sandstones that comprise a net upward

coarsening and bed-thickening succession. The constituent storm-dominated, marine parasequences typically shallow from the offshore transition zone to just above fair-weather wave base. The intensity of bioturbation is highly variable (5-25%), but is highest in association with clay-rich lithologies, and shows a net decrease in intensity through the coarsening-upward shallowing cycles in the Stainmore Formation.

The trace fossils were first described more than 150 years ago (Tate, 1859). The original description of the assemblage included introduction of *Crassopodia embletonia* (a *nomen oblitum*) and *C. media* (a *nomen dubium*) that were subsequently synonymized with *Psammichnites plummeri* and *Psammichnites implexus* respectively (Mángano and Rindsberg 2003). Herein we apply the serial grinding and modeling techniques of Bednarz et al. (2015) to study the morphology of *Parataenidium* (*Eione*) *moniliformis*. Serial grinding and digital reconstruction were used to produce: 1) detailed high-resolution three-dimensional models; 2) to reconstructions of the internal and external morphology of *N. moniliformis*; and models of the interaction between the trace fossil and the surrounding sediment. This study aims to thoroughly characterize the morphology of *P. moniliformis*, in order: 1) to clarify its current taxonomic status; and 2) to provide an updated model for its construction through inferring the possible trace-maker ethology.

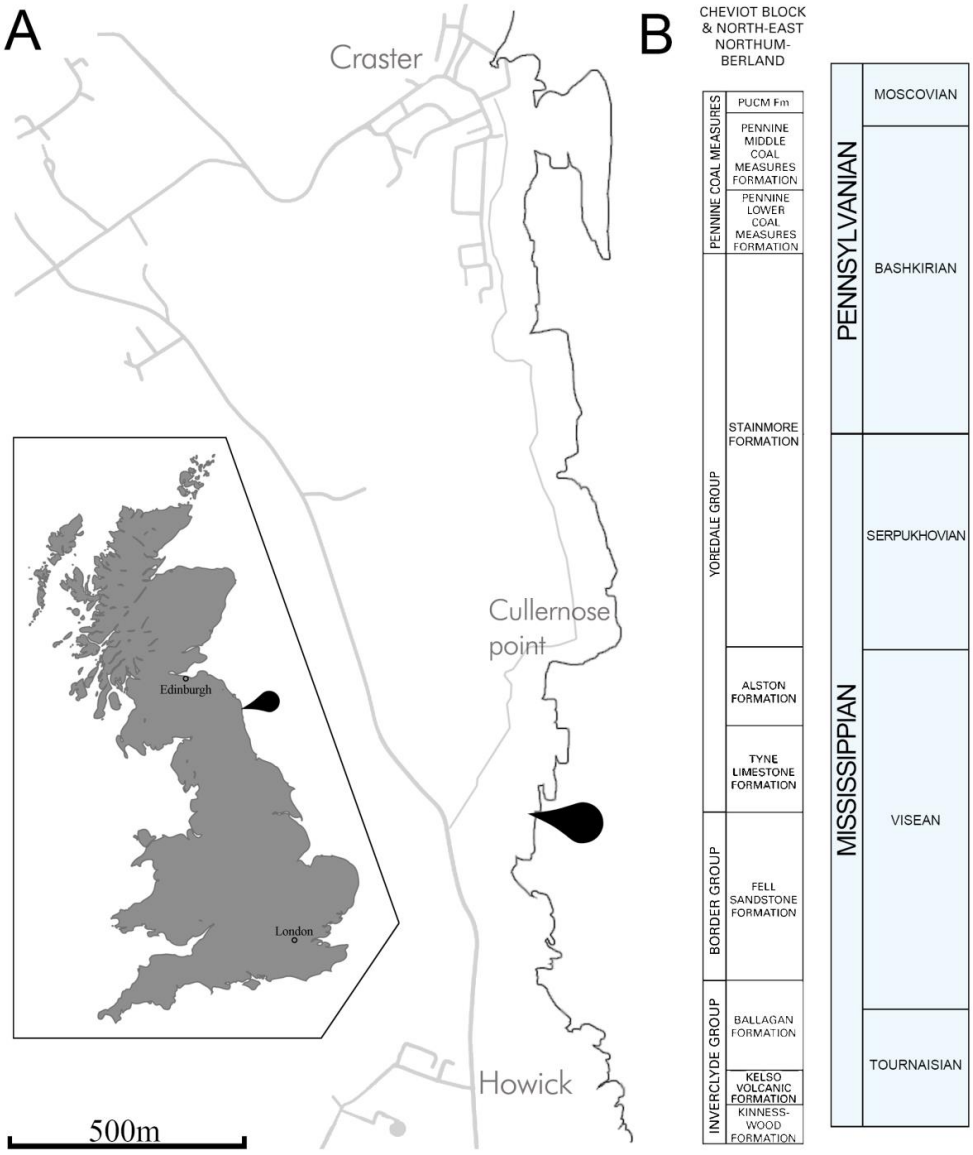

Figure 1. **,** Map of field location, black arrow indicates the sample location from which the material of Tate (1859) was probably also collected (coordinates 55° 27′30.38″ N, 1° 35′34.32″W), which is located along the coast of the between the towns of Howick and Craster. The inset identifies the field location with respect to the greater United Kingdom; **B,** Generalized stratigraphic column showing the Stainmore Formation in relation to the Yoredale Group and others from Northeast Northumberland. Modified from Dean et al. 2011.

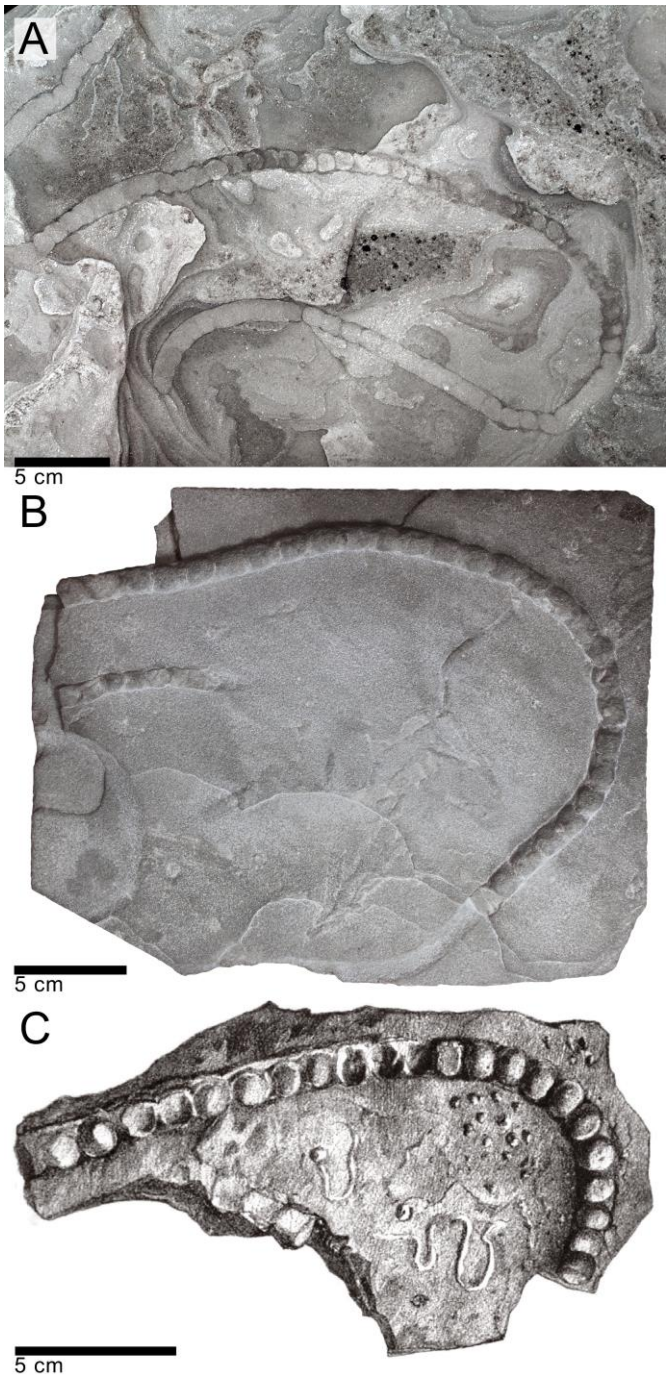

Figure 2. Comparison of: **A,** a field sample collected as part of this study, with (**B**) the neotype of *Parataenidium (Eione) moniliformis* (Tate) BMNH T163 housed at the British Museum of Natural History as designated by Buckman (2001) and photographed by Ms Jill G. Darrell, and a mirror image of the original figure of Tate (1859) demonstrating the morphological and lithological similarities (**C**).

Methodology and Modeling

Field samples of *Parataenidium moniliformis* were described, photographed and collected from closely localized float and *in situ* samples. Of the collected samples, two were analyzed using the methods described by Bednarz et al. (2015). This method involves encasing the specimen in plaster, which is shaped into a rectangular prism, the corners being used for reference points. The sample was then serially ground using a computer guided milling machine in controlled increments of between 0.1-0.3 mm using a diamond carbide grinding tool. After each subsequent increment of grinding the sample was removed from the machine, cleaned, wet with oil, and photographed. The stack of digital images was processed for consistent color and digitally aligned using Adobe Photoshop®. Sedimentary structures of interest (burrows, sedimentary layers etc.) were then selected and extracted from their background image and exported separately. The series of extracted images of the isolated structures were then modeled using volume graphic image software (VGStudio Max®). The voxel dimensions were calculated manually from scale images and grinding intervals to produce a high-resolution three-dimensional model that could be manipulated in three dimensions and digitally sectioned in any plane. For this study the extracted images were selected so as to retain the original color, which allowed for easy visualization of lithological differences. In addition to modeling the selected burrows, models were produced of the entire rock volume, allowing virtual sectioning of the entire sample in any plane to view the burrows in context of the surrounding sediment. This type of analysis can elucidate morphological elements that are

often absent in the crack-out or weathered specimens generally used by ichnologists. Fine-resolution serial grinding also allows detailed study of the internal structure of the burrows as well as the surrounding sediment.

Two samples from the type locality of Buckman's *Parataenidium moniliformis* were serially ground and photographed for this study; the primary sample contained two *P. moniliformis*, whereas the second sample contained a specimen of aff. *P. moniliformis*. The grinding increment for the primary sample was initially set to 0.3 mm but was decreased after 36 grinds to 0.1 mm to increase resolution. The grinding increment for the secondary sample was 0.3 mm throughout.

Taxonomic background: from *Eione* to *Parataenidium*

The ichnogenus *Eione* was established in 1859 by George Tate as a part of his study of the geology and paleontology of the Beadnell area in the United Kingdom (Tate, 1859). Tate initially considered *Eione* to be the fossilized remains of an annelid-like creature that reached upwards of three feet in length, but was confused by the absence of any setae, cirri, appendages, and internal structure (Tate, 1859). One year previously, Hancock (1858) described "nodulous tracks" comparable to *Eione* from a private collection but as he considered it to be a burrow rather than a preserved organism he did not provide a name for it. Hancock (1858) considered the burrows to have been produced by an amphipod similar to *Pontocrates arcticus* after observing the formation on the beach of

what he deemed similar tracks. Tate (1859; p.68) stated that *Eione* was found at 'Howick, Scremerston, and Haltwhistle in Northumberland, and I believe also in Yorkshire'. The holotype material as originally figured cannot be positively identified in Tate's collections, but Buckman (2001) selected a neotype, BMNH T163, thought to have been collected by Tate. The hand-drafted image in Tate's paper strongly resembles a reflected version of BMNH T163 with some liberties taken on the outline of the rock slab and some minor details of the slab surface, as is common in works of that period. The neotype sample location is listed as Yorkshire, but considering the lithological similarities with the Stainmore Formation sandstones, and Tate's phraseology, we consider it most likely to have originated from near Howick.

Forty-five years prior to Tate's description of *Eione*, Rafinesque (1814) named a genus of gastropod *Eione*. Since *Eione* Tate was introduced for a new genus of animal, despite its subsequent assessment as a trace fossil, it continues to compete in homonymy (ICZN 1999, Article 2.2), therefore requiring a new name (Benton, 1982; Rindsberg, 1994; Mángano et al., 2000; Buckman, 2001). Buckman (2001) created *Parataenidium* for backfilled tubular traces that consist of two separate layers in order to accommodate *Eione* Tate (Buckman, 2001) and the new type species *Parataenidium mullaghmorensis* Buckman, 2001. This work provides the first detailed reconstruction of *Parataenidium moniliformis* for comparison with the type material and ichnogeneric diagnosis of *Parataenidium*.

Descriptive ichnology

In order to compare *Parataenidium moniliformis* with the type species *P. mullaghmorensis*, this study describes *P. moniliformis* in detail and assesses its position with respect to the ichnogeneric diagnosis of *Parataenidium. Parataenidium moniliformis* occurs as chains of sand-filled, mud-lined, subspherical sediment packages that are 0.5-1.75 cm in width. Burrow chains can be longer than 85 cm, are commonly highly sinuous (sinuosity index greater than four; Fig. 2A), and are not restricted to a single bedding plane (Fig. 3). Although *P. moniliformis* tends to remain within a particular bed, it has been documented as crosscutting beds obliquely upward (Fig. 3). The burrow also shows a subvertical component that tapers and terminates within the sample (Fig. 4A). *Parataenidium* has not previously been documented to exhibit any form of branching; however, a small portion of a burrow displays secondary successive branching (Fig. 4A,B; cf. D'Alessandro and Bromley, 1987). The longest burrow modeled is approximately 120 mm long, 9 mm wide, 7 mm high, and composed of 22 sediment packages arranged roughly parallel to bedding, with only a small portion of the burrow inclined steeply to bedding (approximately 55^{o}) (Fig. 4A). The sediment packages within *P. moniliformis* are composed of clean sandstone though the lower portion may be clay-rich (Fig. 5). The upper portion of the sediment packets is generally thickly lined with mud on both the sides and top, but the junctions between the packets and the lower boundary of the burrow is commonly thinly lined (Figs. 5, 6B).

The sediment packages of *Parataenidium moniliformis* are either broadly spheroidal ovoid or reniform. Successive sediment packages demonstrably crosscut older packages, creating a chain of overlapping bulbs, each having a lagging rounded edge and a leading flat or cylindrical edge positioned under the rounded edge of the subsequently formed sediment package (Figs. 5, 6, 7). The dimensions of each sediment packet within a single burrow are usually relatively consistent, but the morphology in bedding-parallel cross section can vary along the length of the burrow from spherical to crescentic, gibbous, or oblate depending on the plane of intersection and the alignment of adjacent sediment packets (Figs. 4, 6A). In longitudinal cross sections taken perpendicular to bedding, the long axes of the sediment packets are typically inclined to give an imbricated appearance (Figs. 3, 6B). The lateral margins of burrows are typically irregular and exhibit a broadly corrugated pattern (Figs. 4, 6A). When sectioned transversely, the burrows commonly appear to have a distinct lower level that is isolated from the sandy upper portion (Fig. 7) and comparable to the lower portion of *P. mullaghmorensis* (cf Fig. 7A). When assessed in three dimensions it is clear that the lower portion is the result of cross-sectioning the arcuate lower surface of adjacent sediment packages (Figs. 6, 7). It is clear therefore that the apparent "lower level" of *P. moniliformis* is a cross-sectional artefact and dissimilar to the "repichnial portion" of *P. mullaghmorensis* (cf. Fig. 7). As such it is clear that *Parataenidium mullaghmorensis* is morphologically dissimilar and was produced in a different manner to the taxon hitherto considered to be *Parataenidium* (*Eione*) *moniliformis*. As such *Parataenidium* remains a valid ichnotaxon, with *Parataenidium mullaghmorensis* as its type ichnospecies, but *moniliformis* does not belong within *Parataenidium* and thus we name it *Neoeione* igen. nov. below.

Figure 3. *Neoeione moniliformis* showing mud-rich outer layer and a series of broadly globular sandstone packages: Bedding-perpendicular cross section through a *Neoeione moniliformis* that cuts through a bedding plane.

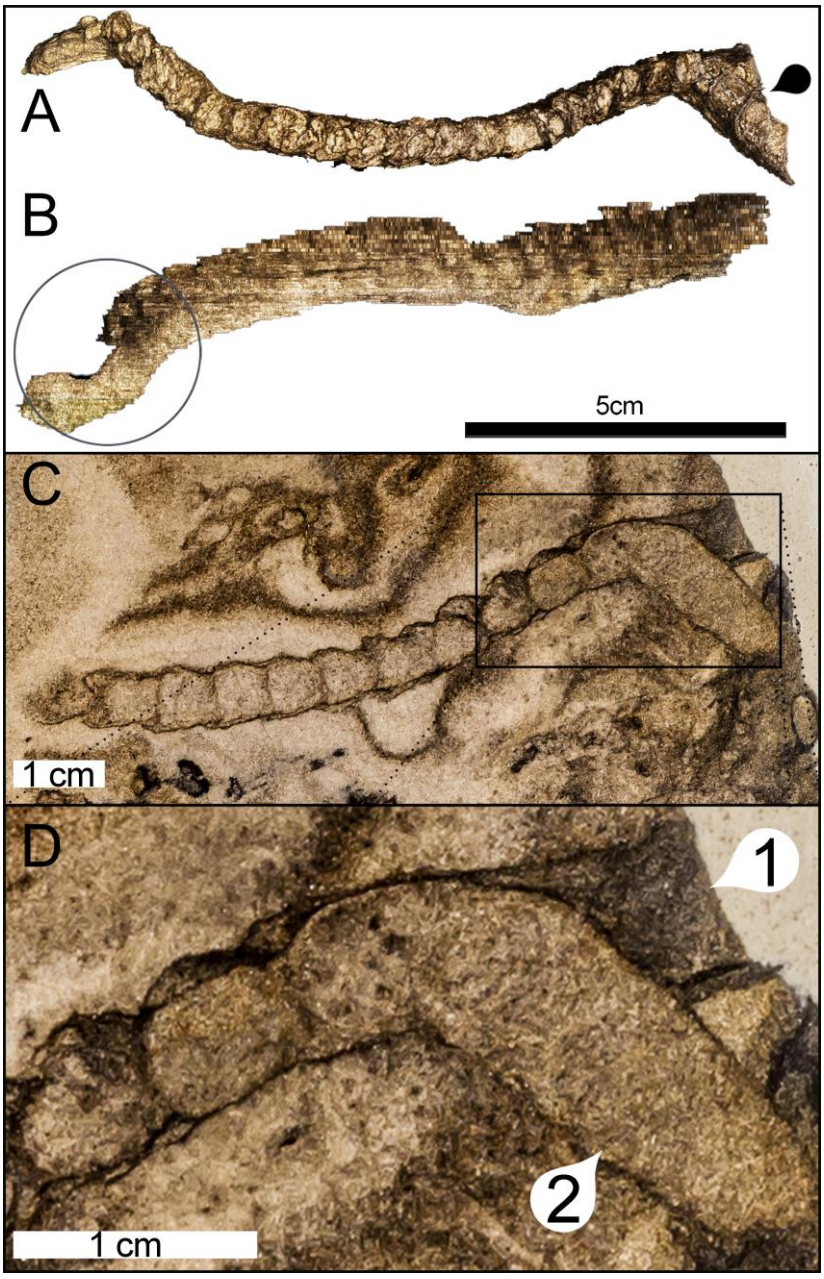

Figure 4. Modeled specimen of *Neoeione moniliformis* igen. nov., comb. nov., as viewed from above, bedding parallel (**A**) and perpendicular (**B**). Occurrence of secondary successive branching indicated by the black icon. Steeply inclined sub-vertical burrow termination enclosed in grey circle. **(C)** Secondary successive branching observed in *Neoeione moniliformis* igen. nov., comb. nov., from a topotype. **(D)** The second branch (2) crosscuts the first (1).

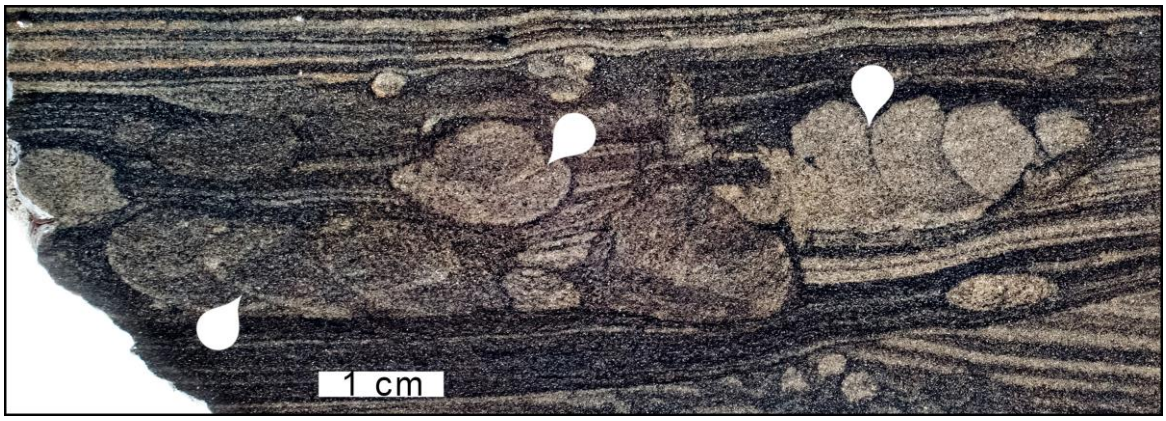

Figure 5. The cross-cutting backfilled sediment packages of *Neoeione moniliformis* igen. nov., comb. nov., displaying variable contents of clay. The junctions between the burrow sediment packages (indicated by white icon) are often thinly lined with clay.

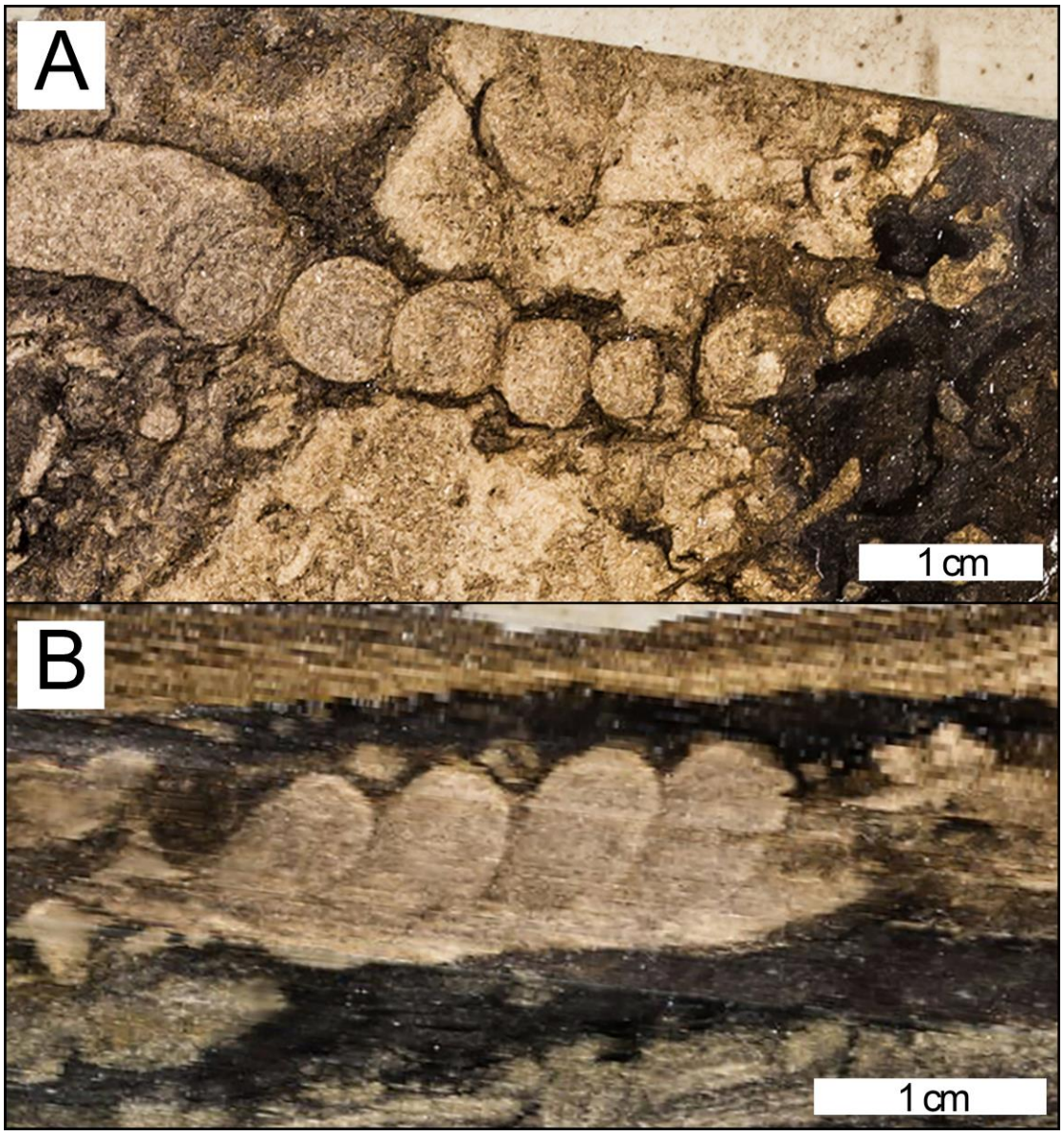

Figure 6. A, Top down, bedding-parallel view of *Neoeione moniliformis* igen. nov., comb. nov., displaying variability in sediment package morphology and lateral variability of successive packages; **B,** longitudinal cross section produced from modeling stacked grind images.

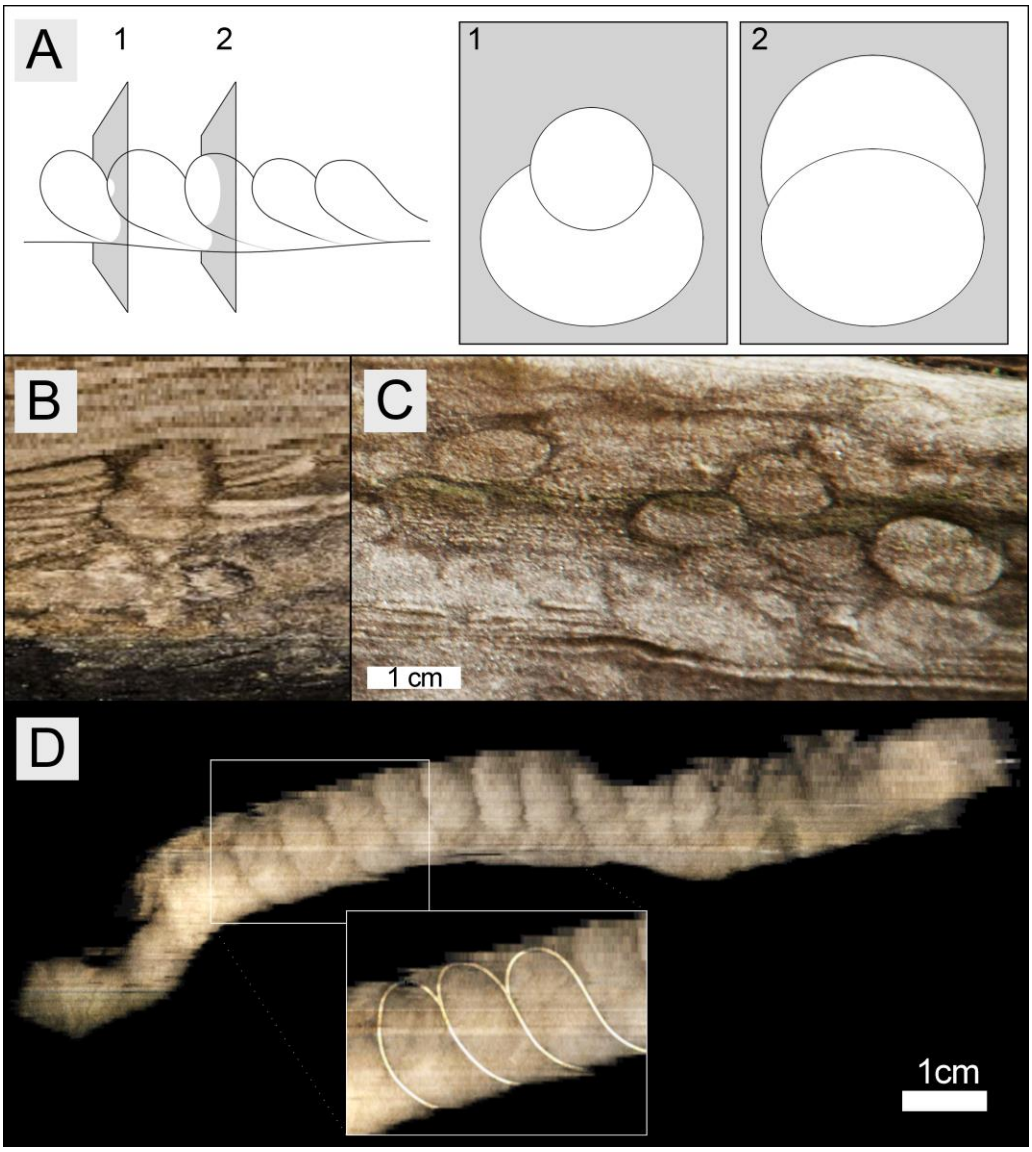

Figure 7. *Neoeione moniliformis* igen. nov., comb. nov. is composed of a chain of backfilled inclined sediment packages within only one level despite its superficial appearance. **A,** Transverse sections of the backfilled sediment packages of *N. moniliformis* can give the false impression of two distinct levels, the proportions of which vary greatly depending on the plane of intersection (1, 2); **B,** Transverse section produced from modeling stacked grind intervals; **C,** Field photograph of transverse sections; **D,** X-radiograph-like rendering of detailed spatial relationship of sediment packages within *N. moniliformis* burrow highlighting the lack of two distinct burrow levels.

Systematic Ichnology

Ichnogenus *Neoeione* new ichnogenus

non 1814 *Eione* Rafinesque p. 155.

non 1826 *Eione* Risso: p. 121.

non 1961 *Petromonile* Casey: p. 600.

non 1967 *Cylindrichnus* sp. Bandel: p. 6.

non 1969 *Cylindrichnus* sp. Bändel; Glaessner: 380, fig. 5a.

Type ichnospecies.— *Eione moniliformis* Tate, 1859.

Other ichnospecies.— *Neoeione seymourensis* (Uchman and Gaździcki, 2006).

Diagnosis.— Straight to sinuous primarily horizontal to subhorizontal trace fossil composed of inclined backfilled sediment packages which crosscut one another giving the appearance of an upper beaded surface, with a shared smooth lower surface. Rarely displays subvertical components and secondary successive branching.

Etymology.— The Greek prefix "neo" meaning new was added to *Eione* forming *Neoeione* to connect the new ichnogenus with its original name *Eione* Tate following its distinction from *Parataenidium* Buckman.

Remarks. — The ichnogenus *Neoeione* is established herein to accommodate *Eione* Tate, 1859, the junior homonym of *Eione* Rafinesque, 1814. *Parataenidium seymourensis*

Uchman and Gaździcki was established on the basis of a single highly weathered specimen collected from Seymour Island, Antarctica (Uchman and Gaździcki, 2006). Despite the poor quality of the specimen, it demonstrates many morphological similarities to *Eione moniliformis* Tate, and appears to be composed of a single layer. It is tentatively reassigned to *Neoeione* on this basis. Examination of topotype would be beneficial in determining the differentiating criteria from *Eione moniliformis* Tate, 1859.

Neoeione moniliformis (Tate, 1859)

Figures 2–8

1858 Nodulous tracks; Hancock: 458-460, pl. 15 (4), pl. 17.

1859 *Eione moniliformis* Tate: 68, pl. 1 (6).

non 1928 *Hormosiroidea* Schaffer: p. 214.

? *1935* Worm castings; Shrock: 175, fig. 1.

1941 Large gastropod trails; Teichert: 385, fig. 4.

1955 Trails; Westoll et al.: 91, fig. 2.

non *1975 Taenidium* Heer; Häntzschel: p. 112.

1984 Constricted burrows; Archer: 287, fig. 4cE.

non 1984 *Margaritichnus?* Bandel; Narbonne: 407, fig. 6c.

? 1985 *Muensteria* Sternberg; Eagar et al.: 116, pl. 6, fig. c.

1987 *?Margaritichnus* Bandel; Lockley, et al.: 258, fig. 3a-c.

1989 "*Eiona sp*"; Devera: 68, pl. 2.

1990 *Eione* ichnosp. Tate; Maples and Suttner: p. 869, fig. 12.9, 13.

1990 *Margaritichnus reptilis* Hakes; Seilacher: pl. 32.3f.

1994 *Eione moniliformis* Tate; Ainsworth and Crowley: 687, figs 7a, 9.

non 1996 *Eione;* Mángano et al.: p.133.

non 1998 "*Eione*" *moniliformis*; Głuszek: 528, fig. 8.

. 2001 *Parataenidium moniliformis* Tate; Buckman: 86, figs 2,5,6,7,8,9c.

2004 *Parataenidium moniliformis*; Mángano and Droser: 378, fig. 34.3a.

2007 Margaritichnus; Seilacher: 53, pl. 17.

2008 *Parataenidium moniliformis*; Baucon and Carvalho: 94, fig. 6.

2012 Parataenidium; Knaust: 85, 89f.

2013 Parataenidium; Šimo, and Tomašových, p. 366.

Neotype. — BMNH T163 (Buckman, 2001).

Diagnosis.— Straight to sinuous, predominantly horizontal to subhorizontal trace fossil backfilled with inclined, clay or silt lined, sediment packages that crosscut one another. Upper surface is a series of broadly trapezoidal protrusions. Lower surface is smooth and convex. Successive branching and subvertical portions are rarely present.

Description. — Burrows are commonly winding and 0.5-1.75 cm wide, forming long chains (in excess of 85cm) of inclined packages that are ovoid to reniform in shape. Burrows can occur in moderate densities but tend not to self-cross, although secondary successive branching has been observed. The burrows are predominantly bedding-parallel, but can include short sub-vertical, sections. Packages are composed of sandier fill with clay lining and are inclined approximately 30-60 degrees from horizontal. The upper portion of the sediment packages are commonly prominently lined while the lower

and the adjoining portions exhibit only a thin lining. The sediment packages tend to be fairly consistent in their broad form but display variation in their specific morphology.

Remarks. — *Parataenidium moniliformis* is reassigned as *Neoeione moniliformis* comb. nov. following the discovery that it is composed of a single level. As these burrows are not composed of multiple distinct levels, *Neoeione moniliformis* is significantly different than the type species of *Parataenidium*, *P. mullaghmorensis*, and does not conform to the diagnosis of *Parataenidium* (cf. Buckman, 2001).

The terminal portion of a probable *N. moniliformis*

The second sample processed for this study contained a burrow that shares many characteristics with *Neoeione moniliformis* igen. nov., comb. nov. (Fig. 8). It is composed of a chain of bulbous sedimentary packages of sediment that terminate at an erosive sediment boundary within the sample. The serial chambers of this probable *N. moniliformis* burrow are approximately 10 mm in diameter and are clay-lined. The contents of the chambers are typically heterogeneous sand and clay. The laminae surrounding the burrow chambers are highly distorted and are pushed up around the burrow chambers (Fig. 8).

Unlike commonly preserved *Neoeione moniliformis* burrows described above, this structure has been reworked by an organism that created two parallel meniscate tunnels on the lower surface of the burrow (Fig. 8). These tubes are filled with clean sand and have a prominent clay lining. Each tube has a 3-4 mm diameter, and they converge into a

single meniscate tunnel with a diameter of 10 mm (Fig. 8). This structure is interpreted as the terminal portion of a probable *Neoeione moniliformis* that was reworked by another tracemaker.

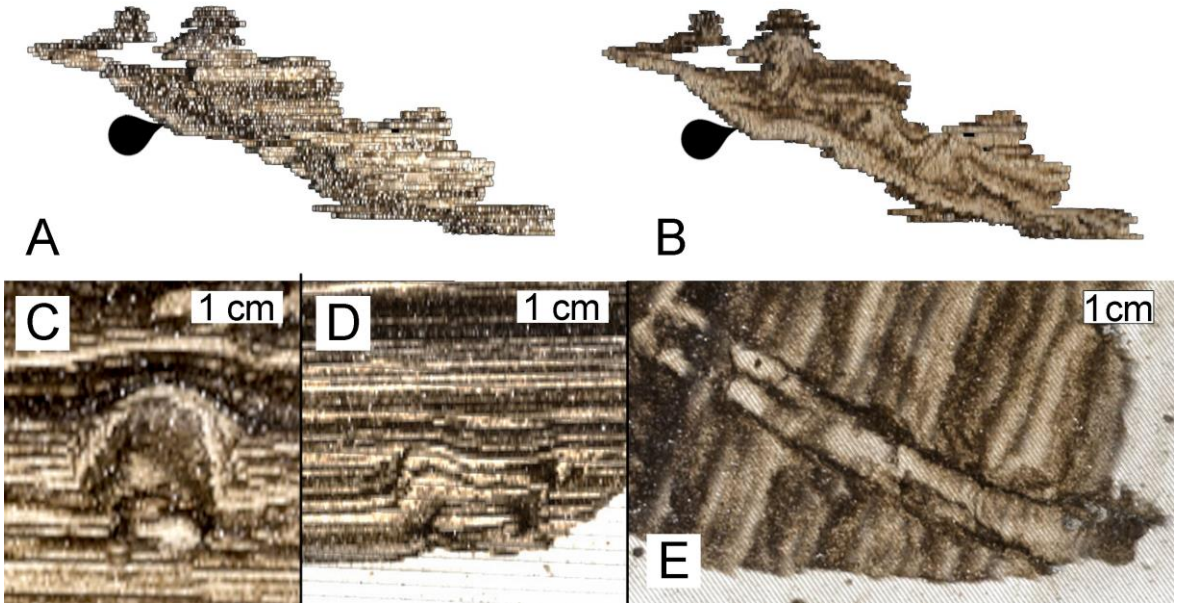

Figure 8. Terminal portion of a probable *Neoeione moniliformis* **A-C,** The beaded appearance of upper surface (**A**) resulting from the uplift of sediment inside the burrow (**B**), deflecting the enveloping sediment (**C**); **D**, Post-construction, the burrow chambers collapse; **E**, Top-down longitudinal section of cross-cutting burrow which reworked the probable *N. moniliformis* burrow (indicated by the black icons in **A** and **B**).

Palaeobiology

The model proposed by Buckman (2001) to describe the formation of the different components of *Parataenidium* (Fig. 9A) invokes an organism moving through the sediment with a lobed foot. The component burrow layers were formed by a combination of sediment ingestion and passing material around its body while burrowing. In this model it is the processed material pushed behind the organism that forms the upper beaded surface of the trace fossil (Buckman, 2001). The lower portion of the trace fossil was inferred to have been constructed by the lobed foot of the trace-makers (Buckman, 2001; Fig. 9A). As *Neoeione moniliformis* lacks the two burrow levels seen in the reconstructions of Buckman (2001), the palaeobiological burrowing model he proposed cannot be used to explain the present material.

Our detailed analysis of the burrow, lining, and adjacent sediment interactions suggests a multistage process of creation for *Neoeione moniliformis*. In our model, the trace-making organism moved through the sediment, creating a small cavity ahead of its body within which to process excavated sediment for foodstuff, mainly from fine-grained sediment (Fig. 9B). The trace-making organism likely secreted mucus that aided the adherence of clay grains on the sides of the burrow. Additionally, with increased water pressure inside the burrow, mobile clay grains within the burrow would likely strain against the burrow wall, and permeate the surrounding sediment, resulting in the formation of a passive lining (cf. Herringshaw and McIlroy, 2013; Jumars et al., 2015). However, given the prominence of the mud lining, it is likely that the lining was

composed of fecal material and was actively produced to stabilize the open portion of the burrow (Fig. 9B). This deposition of labile organic material may have facilitated microbial growth, which may have encouraged coprophagous activity leading to secondary successive branching (cf. Fig. 4B).

Bulk-sediment deposit feeding typically involves the ingestion of large amounts of low nutrient content in order for an organism to gain sufficient nutrients (Kemp, 1986). After processing the contained nutrient content, the trace-making organism is considered to have packed sediment behind itself, thereby forming the bulbous sand-rich portions of *Neoeione moniliformis*, before excavating a new volume of sediment in front of the burrow (Fig. 9B).

Evidence from a hypidiomorphic Neoeione moniliformis. — The probable *Neoeione moniliformis* burrow shares many characteristics with *Neoeione;* however, this burrow is composed of irregular chambers dissimilar to the idiomorphic, ovate to reniform sediment packages typical of *Neoeione*. These irregular chambers are surrounded by distorted sediment, are poorly packeted, incomplete, and commonly lack a defined burrow edge (cf. Fig. 8). Upward deflection of sediment laminae around the chambers suggests that the mechanism of deformation is partly one of inflation during burrowing (cf. McIlroy and Heys, 1997). These chambers commonly show irregularly laminated burrow fills, and evidence for chamber collapse (Fig. 8D). The subtle morphological variation resulting from size and positioning of adjacent chambers, the rheological response of the

surrounding sediment, and the inconsistent degree of chamber collapse highlights the difficulty in using chamber morphology as a reliable ichnotaxobase.

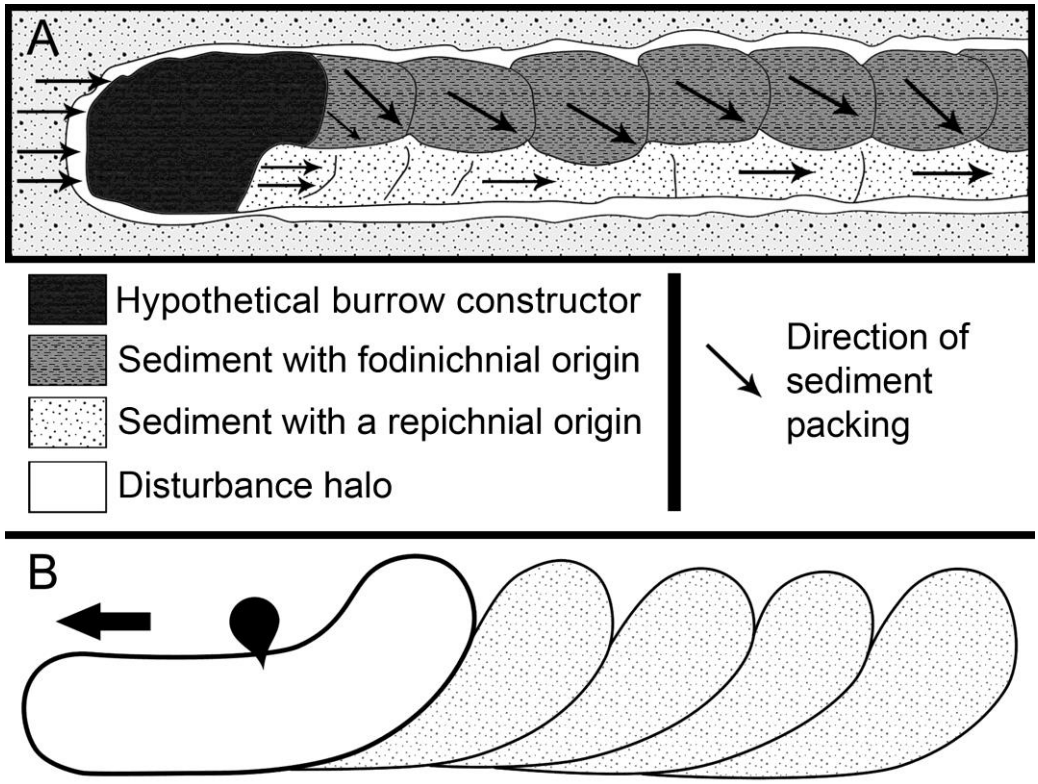

Figure 9. **(A)** Method of formation proposed for *Neoeione* (*Parataenidium*) *moniliformis* (redrafted from Buckman, 2001). **(B)** Newly proposed model of formation of *Neoeione moniliformis*. The trace-making organism maintains an open portion of its burrow (indicated by black icon), where it deposit-feeds on excavated sediment. Processed sediment, including any discarded or egested material, is packed behind the organism. Black arrow indicates direction of burrow propagation.

Conclusion

The description of *Eione* provided by Tate (1859), along with his highly detailed sketches, provides ample information for proper diagnosis. Although *Eione* Tate was originally classified as an animal, any name that has ever been considered as animal continues to compete in homonymy with respect to zoological nomenclature (ICZN, 1999, Art. 2.2). As the name *Eione* had been previously applied to a genus of gastropod (Rafinesque, 1814), which has priority, *Eione* Tate is a junior homonym of *Eione* Rafinesque. The ichnogenus *Parataenidium* Buckman, 2001 was created to accommodate backfilled tubular traces that are divided into two distinct levels. *Eione moniliformis* Tate was transferred to *Parataenidium* on the basis of it being composed of two distinct levels and being morphologically similar to *P. mullaghmorensis* Buckman, 2001. This transfer is herein demonstrated to be problematic for several reasons. Primarily, *Eione* Tate is composed of one, not two distinct layers, though it appears to be made of two when transverse cross-sections cut through two adjacent imbricated chambers (Fig. 7). *Neoeione* igen. nov. is therefore erected to accommodate material originally included in *Eione* (Tate). Although *P. mullaghmorensis* is superficially similar to *Neoeione moniliformis*, *N. moniliformis* has only one distinct level (Fig. 7), and lacks the complexity of *P. mullaghmorensis*. The three-dimensional morphology of *P. mullaghmorensis* is in need of further examination to fully understand its distinctive morphology and the ethology responsible for its formation. Herein we also transfer *Parataenidium seymourensis* (Uchman and Gaździcki) to *Neoeione seymourensis* comb.

nov. Given the highly weathered nature of the holotype, the type locality should be revisited and topotype material should be examined and sectioned to check for the lower burrow level diagnostic of *Parataenidium*, and to better characterize the chamber morphology for comparison with *N. moniliformis*.

Considering the lithological similarities between the neotype and the description and phraseology provided by Tate (1859), we consider the type locality of *Neoeione moniliformis*, igen. nov., comb. nov., to be the coastal outcrops of the Stainmore Formation near the town of Howick, Northumberland, United Kingdom (Fig. 1). We accept the neotype of *Neoeione moniliformis* that Buckman designated (2001) as the probable holotype originally described by Tate, given the strong resemblance of the reflected image and the artistic liberties likely to have been taken with the outline of the rock slab and surface details.

Acknowledgements

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CHAPTER FIVE

Systematic Ichnology of the Stainmore Formation near Howick, Northumberland, United Kingdom.

(Prepared for submission to Proceedings of the Yorkshire Geological Society)

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KEYWORDS

Systematic ichnology; Stainmore Formation; ichnotaxonomy

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ABSTRACT

The ichnological assemblage from the interbedded heterolithic sandstone and siltstone costal outcrops near Howick, Northumberland United Kingdom, is exceptionally well preserved. The first systematic study of the trace fossils of the Stainmore Formation was completed over 150 years ago. This early study was one of the first formal descriptions of an ichnological assemblage found in the literature and predates the common application of the concept of trace fossils. The study presented herein aims to provide an updated systematic ichnological treatment of the ten ichnospecies present in the assemblage. These ichnotaxa are: *Beaconites capronus*; *Chondrites intricatus; Dactyloidites jordii; Megagrapton* isp.; *Neoeione moniliformis; Nereites irregularis; Nereites missouriensis; Psammichnites plummeri; Rhizocorallium commune* (*auriforme,* and *irregulare ivars.*)*;* and *Teichichnus stellatus.* The described ichnotaxa represent a diverse assemblage that includes trace fossils inferred to have been produced by as dwellings as well as a range of feeding strategies including grazing, deposit feeding, and potential farming.

INTRODUCTION

The interbedded Carboniferous sandstone and siltstone beds of the Stainmore Formation near Howick in Northumberland contain a diverse suite of well-preserved trace fossils. The clay-rich heterolithic sediment preserves subtle details that provide unique information on the mode of burrow formation and inferred mode of life of the trace-makers. The first study of the fossils near Howick was originally undertaken over 150 years ago (Tate 1859). This first account of the fossils considered them to be body fossils of annelids, which was common in many contemporary studies (cf. von Schlotheim, 1822; Brogniart, 1823; Binney, 1852; Salter, 1856) and predates the common application of the concept of trace fossils (cf. Narthorst, 1881, Richter, 1927; Osgood, 1975; Baucon *et al.*, 2012). This study provides an updated database of the diverse and well-preserved ichnological assemblage in the coastal outcrop of the Stainmore Formation, and enhances the understanding of the palaeoecology and palaeoenvironment of the Stainmore Formation.

Geological and palaeoenvironmental setting.

The Stainmore Formation was deposited as a part of the Yoredale Group throughout the Serpukhovian and into the early Bashkirian (Dean *et al*. 2011). This study concerns the ichnological assemblage found within the coastal cliffs approximately one kilometer North of Howick, Northumberland located at 55° 27’30.38”N, 1° 35’34.32”W (Figure 1). This succession belongs to the Bashkirian age section of the Stainmore

Formation and is typically composed of inter-bedded sandstone, siltstone, mudstone, and limestone wave/storm dominated parasequences (Dean *et al.* 2011).

The inter-bedded sandstones and siltstones range in thickness from cm to dm and display a net upward-coarsening trend that is itself composed of several upward coarsening parasequences. The inter-beds are composed of alternating clean sandstone and clay/mica rich siltstones rich in illite, muscovite, biotite, and chlorite/serpentine of both detrital and diagenetic origins. The clean sandstone units commonly exhibit trough cross bedding as well as hummocky cross-stratification, particularly in the thicker units. The trace-fossil rich portion of the succession is dominated by hummocky cross stratified sandstones and tempestites and is considered to have been deposited as a part of a storm-dominated marine shoreface succession, between the fair-weather wave base and storm wave base. The intensity of bioturbation generally ranges from 5-20% with localised zones of intense bioturbation of approximately 90% in association with clay-rich mudstone beds.

The findings presented herein are based on field observations and photographs as well as numerous samples collected from closely localised float. Specimens were analysed using petrographic thin sections, as well as using the three dimensional modelling techniques described by Bednarz *et al.* (2015).

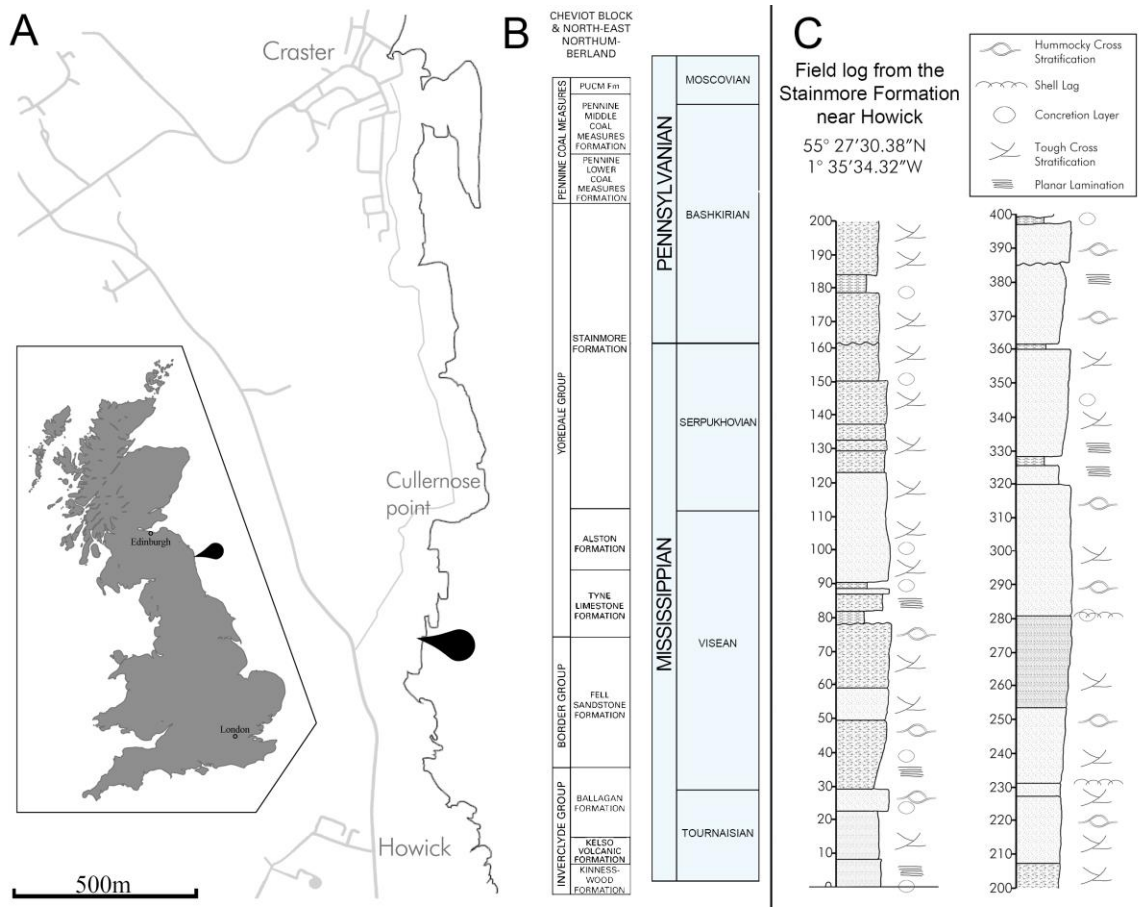

Figure 1. A) Black icon indicates the location of the coastal outcrop of the Stainmore Formation situated between the towns of Howick and Craster (55° 27'30.38"N, 1° 35'34.32"W) relative to the United Kingdom (map inset); B) Generalised stratigraphic column showing the Stainmore Formation, part of the Yoredale Group. The outcrop near Howick is from the Bashkirian portion of the Stainmore Formation. Modified from Dean et al. (2011). C) Sedimentary field log of the Stainmore Formation located near the town of Howick, Northumberland indicated by the icon in (A).

SYSTEMATIC ICHNOLOGY

Ichnogenus **BEACONITES** Vialov, 1962

Type ichnospecies. Beaconites antarcticus Vialov, 1962 (by monotypy).

Diagnosis. Small, cylindrical, walled, meniscate burrow occasionally exhibiting secondary successive branching. Straight or sinuous, horizontal or more rarely inclined or vertical. Weakly to strongly arcuate meniscate packets or segments enclosed by distinct, smooth and unornamented burrow linings (after Keighley & Pickerill 1994).

Remarks. The differentiating diagnostic feature that separates *Beaconites* from the morphologically comparable ichnotaxa *Taenidium* and *Ancorichnus* is the presence of a prominent burrow lining (Keighley & Pickerill 1994). Examination of topotype material of the type ichnospecies, *B. antarcticus*, mentioned the presence of only a weak lining (Bradshaw 1981). The presence of only a poorly developed lining is an insufficient differentiation from *Taenidium* (Goldring & Pollard 1995; Retallack 2001). Although further examination of the type ichnospecies is required, we maintain the name *Beaconites*, as emended by Keighley and Pickerill (1994), as a useful name that should remain in use.

Beaconites capronus (Howard & Frey, 1984): Keighley & Pickerill, 1994 Fig. 2

Emended diagnosis: Predominantly horizontal to sub-horizontal, straight to sinuous, lined cylindrical burrows with chevron-shaped meniscate back-fill. Typically does not self-cross and does not display true branching, but occasionally exhibits secondary successive branching. Rare vertical pipes with identical lining and meniscate fill may be present.

Description. Horizontal winding burrows with connecting vertical shafts. Burrows are back-filled with heterolithic meniscate back-fill of distinct chevron shape (Figure 2). The burrow fill is variable; with some burrow segments being filled by predominantly clay rich, fine grained material and others primarily clean sandstone. Burrows exhibit secondary successive branching but do not otherwise self-cross. Burrow widths are relatively constant with diameters of *c*. 7 mm. Burrow lining is composed of clay rich fine grained material with thicknesses between 0.5-1.2 mm. Winding pattern is often broad and sinuous with few relatively tight turns.

Remarks. The type material of *Beaconites capronus* has been misplaced following the passing of Robert Frey (Andrew Rindsberg, pers. comm., 2015). It is recommended that the type locality, the Panther Member of the Star Point Formation in Cordingly Canyon, Utah, be revisited and topotype material be collected included the designation of neotype material.

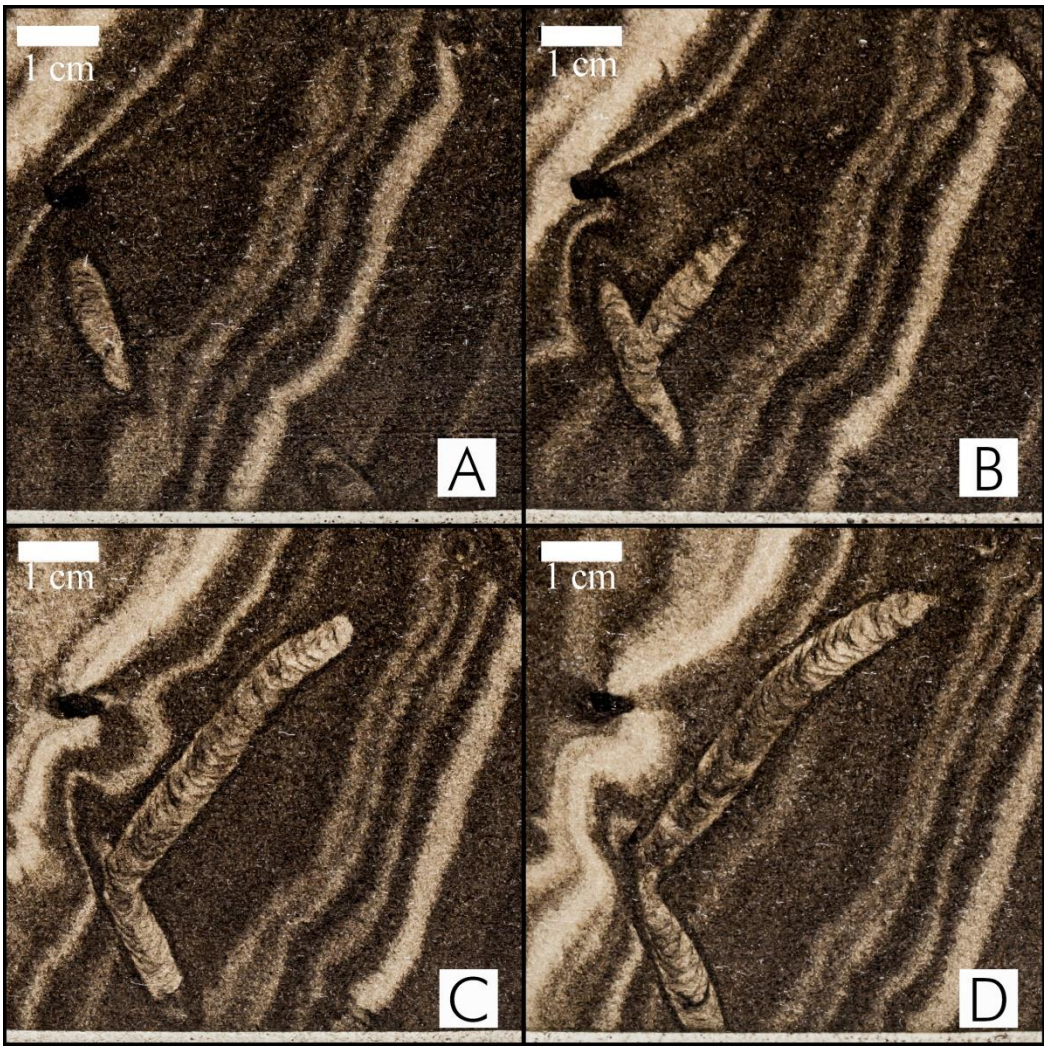

Figure 2. Serial succession of images of *Beaconites capronus* burrows displaying secondary successive branching. Images A-D are separated by 0.6mm between each photograph.

Ichnogenus **CHONDRITES** von Sternberg, 1833

Type Ichnospecies. Chondrites targionii (Brongniart 1828): Von Sternberg 1833

Diagnosis. Regularly branching tunnel systems consisting of a small number of master shafts open to the surface that ramify at depth to form a dendritic network (From Uchman 1999).

Remarks. Chondrites is one of the oldest valid ichnotaxa, dating back to the work of Adolphe Brongniart in 1828. As a result of longstanding misidentification as a fossilized plant, *Chondrites* was in need of thorough revision and review (cf. Fu 1991). *Chondrites* is now generally interpreted to represent the feeding system of an unknown infaunal trace maker that systematically probed the sediment during deposit-feeding activity (*e.g*. Osgood 1970; Uchman 1999). It is considered to be a deep-tier trace fossil created by the feeding activity of a chemosymbiotic organism, and is often used in palaeoenvironmental analysis to suggest dysoxic palaeoenvironmental conditions (Bromley & Ekdale 1984; Savrda & Bottjer 1986, 1989, 1991; Seilacher 1990; Fu 1991). The trace maker may have been capable of tolerating dysaerobic conditions utilizing a vertical shaft connecting to the overlying water column (Bromley & Ekdale 1984; Ekdale & Mason 1988). *Chondrites* has been described from rocks ranging in age from Cambrian to Holocene (*e.g*. Werner & Wetzel 1982; Crimes 1987).

In a relatively recent review, the mode of branching was used as the primary ichnotaxobase for *Chondrites* resulting in over 150 ichnospecies being synonymized into

just four: 1) *C. targionii* Brongniart 1828; 2) *C. intricatus* Brongniart,1828; 3) *C. patulus* Fischer-Ooster 1858; and 4) *C. recurvus* Brongniart 1823 (cf. Fu 1991).

The sole use of the mode of branching as an ichnotaxobase led some authors to consider this revision an oversimplification and morphometric parameters were used as an additional ichnotaxobase (Uchman 1999). Using these morphometric parameters, the ichnospecies *C. stellaris* Uchman, 1999, *C. caespitosus* Fischer-Ooster 1858, and *C. affinis* von Sternberg 1833, were determined to also be valid (Uchman 1999; Uchman *et al.* 2012).

Chondrites intricatus (Brongniart, 1823): Von Sternberg, 1833 Fig. 3

Diagnosis. Small *Chondrites* composed of numerous downward radiating, mostly straight branches. The angle of branching is usually less than 45^{o}. The branches are less than 1.0 mm (mostly about 0.5 mm) wide. The burrow system is more than 20 mm wide (From Uchman 1999).

Description. Straight downward radiating tunnels display prominent primary successive branching, are relatively consistent in diameter at *c*. 1 mm, and are filled with contrasting sediment material to the host sediment. Multiple orders of branching are common. Angle of branching is approx. 45^{o}, and branches are generally centimetres in length. Specimens were observed in situ and in float. Although dispersed throughout the succession, burrows were commonly observed in silt-rich mudstones.

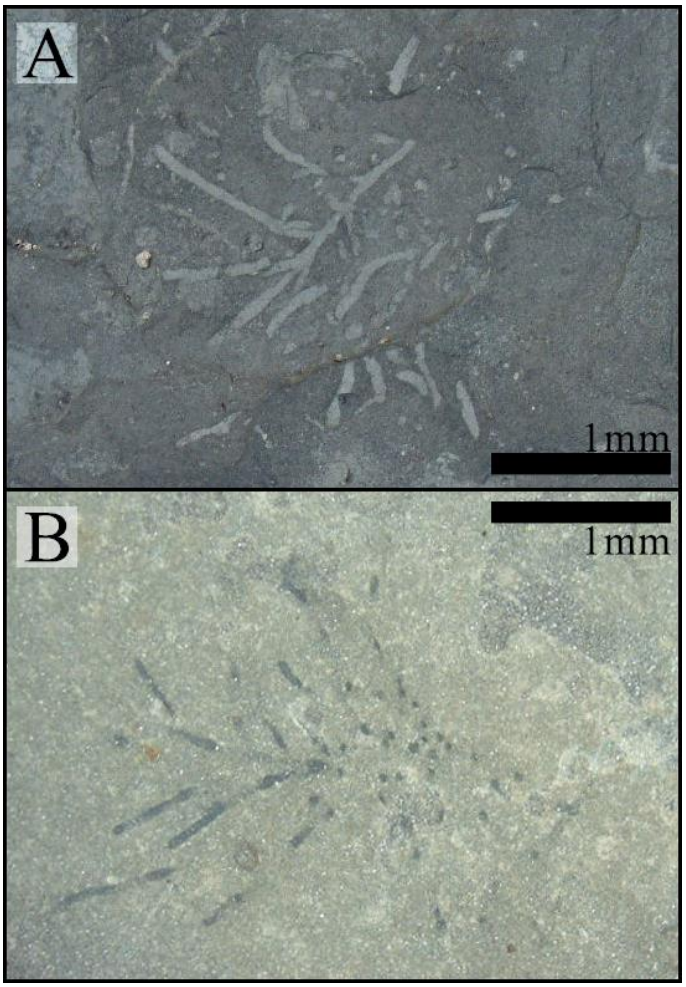

Figure 3. *Chondrites intricatus* with lighter burrow fill in a darker matrix (A) and darker burrow fill in a lighter matrix.

Ichnogenus **DACTYLOIDITES** Hall, 1886

Type ichnospecies. Dactyloidites asteroides (Fitch 1850): Walcott 1898

Emended Diagnosis. Radiating burrow system, forming stellate to palmate rosettes composed of branched or unbranched, actively filled spreiten rays radiating horizontally to sub horizontally from a single vertical to sub-vertical central shaft 5-25 cm long.

Remarks. The ichnogenus *Dactyloidites* has a complicated taxonomic history and was originally considered as the body fossil of a fucoid or a sponge (Hall 1886). The type species, *D. bulbosus*, was later synonymised with *Buthotrephis asteroides* Fitch, 1850 which had priority (Walcott 1898). As the genus *Buthotrephis* was itself invalid, the type species became *Dactyloidites asteroides* (Hall 1886; Fillion & Pickerill 1990). In a recent review of *Dactyloidites* it was considered to be the senior synonym of two other genera, *Brooksella* Walcott, 1896 and *Haentzschelinia* Vialov, 1964 (Fürsich & Bromley 1985). The synonymization of *Haentzschelinia* has been the more contentious of the two (Vialov 1989; Schweigert 1998).

Haentzschelinia was created with two ichnospecies, *H. kolymensis* and *H. pygmea*, with a third being added later following reinterpretation of the sponge *Spongia ottoi* Geinitz, 1849 (Vialov 1964; Häntzschel 1970). All three of these ichnospecies were found to be synonymous and *Dactyloidites (Spongia) ottoi* took priority (Fürsich & Bromley 1985).

Dactyloidites jordii Boyd and McIlroy Fig. 4

Diagnosis. Broadly bisymmetrical trace fossil consisting of radiating burrows that fan out between 70°-180° degrees each side of a central shaft that is orientated oblique to bedding. The burrows may exhibit multiple orders of primary successive branching within a fan, with several fans being arranged in successive tiers that are laterally oblique to one another. The component burrows of the trace fossil are typically 1.5 to 3.5 mm in diameter, range from 3 to 10 cm in length, and can branch both horizontally and vertically.

Description. Complex radially arranged burrow system formed of multi-levelled tiered galleries composed of clean sandstone with a mudstone lined tubes (Figure 4A). Numerous elongated narrow tubes radiate from a central shaft forming incomplete rosettes of between 70-180°. Radiating tubes are approximately 2-3 mm in diameter, 3-10 cm in length, and exhibit three orders of branching (Figure 4B). The burrow system serially ground and modelled for this study clearly demonstrated a bisymmetrical arrangement (Figure 4B; components labelled 1 and 2).

Transverse cross sections of the burrow probes often exhibit an n–shaped morphology.

Remarks. Dactyloidites jordii is morphologically comparable to *D. ottoi* and *D. peniculus* but is distinguished by having numerous relatively narrow radiating tubes, that do no self-cross and having multiple orders of branching. The radiating rosettes of *D. jordii* are typically less complete than those of *D. ottoi* or *D. peniculus.*

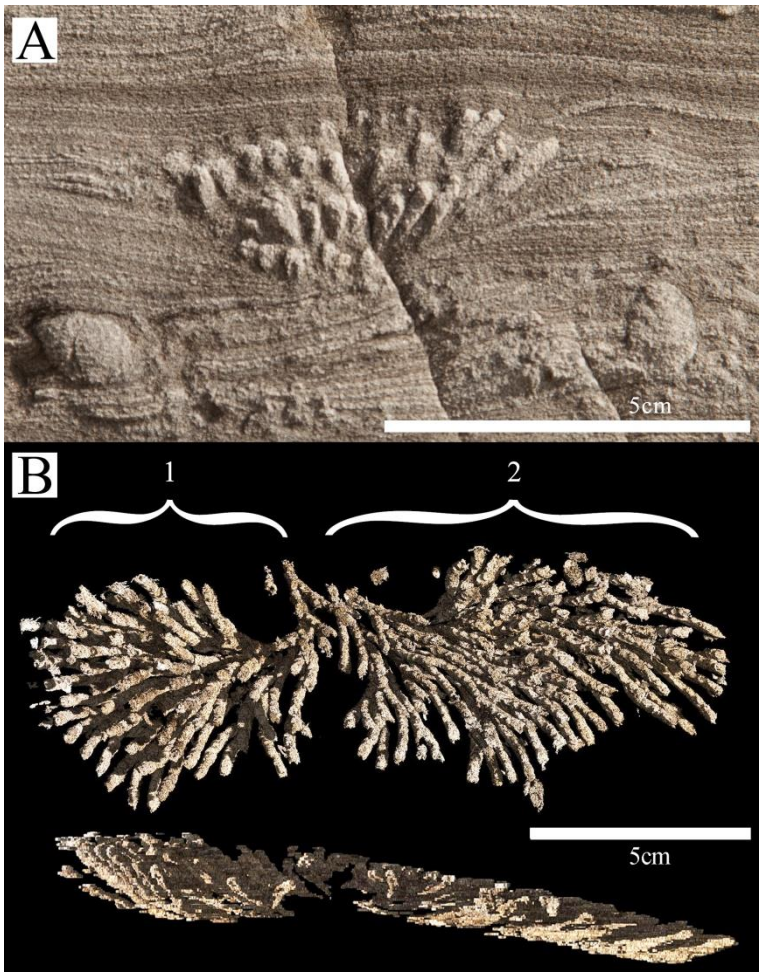

Figure 4. *Dactyloidites jordii* in situ (A) and as modelled using the serial grinding techniques (B). The two components of the bisymmetrical burrow system (labelled 1 and 2) differ in their order of burrow construction. Side 1 resulted from construction under more ideal circumstances; Side 2 represents hypidiomorphic burrow construction inferred to be the result of encountering a food-poor sediment layer.

Ichnogenus **MEGAGRAPTON** Książkiewicz, 1968

Type Ichnospecies. Megagrapton irregular Książkiewicz, 1968.

Diagnosis. Trace fossils commonly preserved as hypichnial irregular nets (From Uchman 1998).

Remarks. Megagrapton was originally described as a curved trace with lateral components that linked to form irregular nets, however this does not accurately describe the figured material presented therein (Książkiewicz 1977; Uchman 1998). *Megagrapton* is instead composed of irregular hypichnial meshes (Uchman 1998). The perceived meanders likely originated with the partial erosion of these meshes (Uchman 1998). In this regard *Megagrapton* is superficially comparable to the ichnogenus *Multina*, however it is differentiated in that *Multina* is actively filled and is an endichnial network (Uchman 2001).

Megagrapton is a relatively simple graphoglyptid representative of early development in the graphoglyptid biodiversification and morphological radiation of the Palaeozoic (*cf.* Uchman 2003).

***Megagrapton* isp.** Fig. 5

Description. Irregular hypichnial polygonal meshes of strings with siliceous burrow fill of even diameter, *c.* 1mm, and irregular micaceous lining, *c.* 0.3 mm.

Complete polygons are rarely preserved leaving isolated burrow strings. Burrows occasionally terminate against micaceous circular structures possibly representing an associated vertical burrow portion (Figure 5).

Remarks. The thinly-lined burrow strings presented herein cross-cut other burrows demonstrating that they were created late in the colonization history of the bed. The lining and post-depositional nature of these burrows are unique when compared to other ichnospecies of *Megagrapton*.

Figure 5. *Megagrapton* consisting of irregular hypichnial polygonal meshes of strings which cross-cut other burrows indicating they were created late in the colonization history of the bed.

Ichnogenus ***NEOEIONE*** Boyd and McIlroy

Type ichnospecies. Neoeione moniliformis (Tate 1859): Boyd and McIlroy

Diagnosis. Straight to sinuous primarily horizontal to sub-horizontal trace fossil composed of inclined back-filled sediment packaged which crosscut one another giving the appearance of an upper beaded surface, with a shared smooth lower surface. Rarely displays sub-vertical components and secondary successive branching.

Remarks. Neoeione burrows were originally described and named *Eione moniliformis* by Tate (1859) who considered them as the fossilized remains on an unknown annelid. The name *Eione* was, however, unavailable given its prior use for the genus of gastropod *Eione* Rafinesque 1814, making *Eione* Tate a junior homonym of *Eione* Rafinesque (Rindsberg 1994; Buckman 2001). This led to *Eione* Tate being included in the ichnogenus *Parataenidium* that was created for horizontal burrows composed of two distinct layers as well as to accommodate the material described by Tate (Buckman 2001). This transfer is problematic primarily due to *Neoeione* (*Eione*) *moniliformis* lacking the two-layered structure required by the diagnosis of *Parataenidium* (Buckman 2001). Despite superficially appearing to have an upper beaded layer as well as a lower cylindrical layer; the beaded back-filled portion of *N. moniliformis* actually extends downward to the base of the burrow.

Neoeione moniliformis (Tate 1859): Boyd and McIlroy Fig. 6

Diagnosis. Straight to sinuous primarily horizontal to sub-horizontal trace fossil. Back-filled with imbricated reniform packages of sand-rich sediment. Packages are inclined away from direction of burrow propagation and crosscut one another giving a beaded appearance to the upper surface and a cylindrical lower surface. Successive branching and sub-vertical portions are rarely present. Sediment packages are commonly prominently lined with fine-grained sediment.

Description. Primarily horizontal to sub horizontal burrow composed of back-filled, beaded, reniform sediment packages (Figure 6). Packages are thickly and irregularly lined and closely spaced giving an imbricated appearance. Sediment packages are inclined away from the direction of burrow propagation and crosscut one another. The adjoining boundary between two sediment packages is often thinly lined, but is demonstrated to connect to the burrow's lower boundary (Figure 6B). Secondary successive branching and sub-vertically orientated portions of the otherwise horizontal burrow are rarely present.

Remarks. The transfer of *Eione* Tate to *Parataenidium* Buckman was based on two factors: 1) *Eione* Tate was a junior homonym of *Eione* Rafinesque and thus required revision (Rindsberg 1994; Buckman 2001), 2) Transverse cross sectioning of *Eione moniliformis* can give the appearance that the burrow is composed of two distinct levels;

an upper faecal level underlain by a locomotory portion (*cf.* Buckman 2001). Upon examination of the three-dimensional morphology of *Eione moniliformis* using serial grinding, photography, and modelling techniques the burrow can be demonstrated to be composed of serially aligned, and cross-cutting reniform sediment packages that have been closely packed, giving an imbricated appearance (Figure 6). When the burrow is cross sectioned transversely near the boundary between two sediment packages the overlying portion of the leading sediment package gives the appearance of an upper level. As *Eione moniliformis* does not conform to the ichnogeneric diagnosis provided by Buckman (2001) and only superficially resembles *Parataenidium mullaghmorensis* (the type ichnospecies) the transfer of *Eione moniliformis* is rejected. The new ichnogenus *Neoeione* is created to accommodate this material.

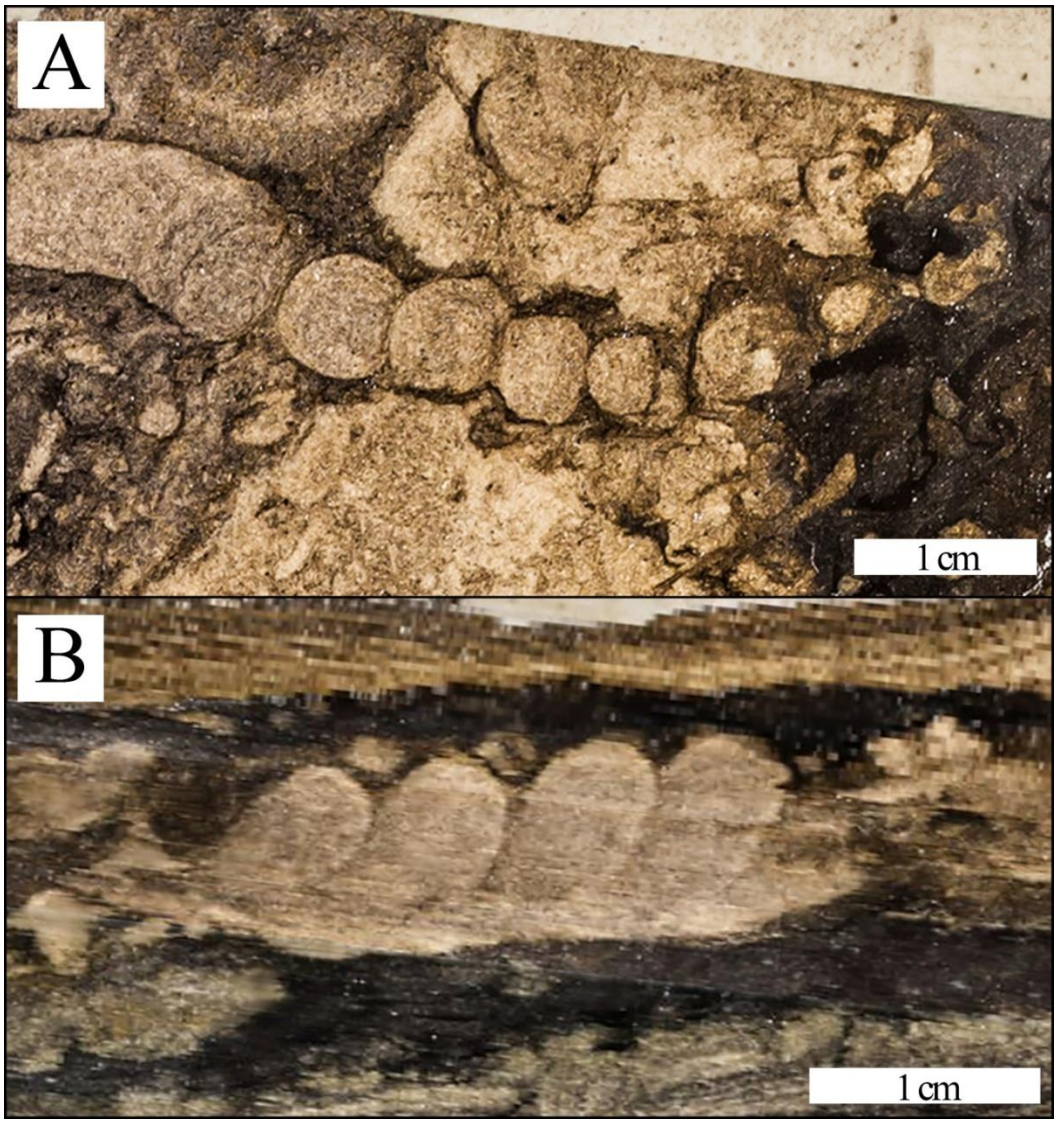

Figure 6. A) Top down, bedding parallel view of *Neoeione moniliformis*, displaying variability in sediment package morphology and lateral variability of successive packages; B, longitudinal cross section produced from modelling stacked grind images demonstrating the burrow is produced by a single level as opposed to having two distinct levels.

Ichnogenus **NEREITES** MacLeay, 1839

Type Ichnospecies. Nereites cambrensis MacLeay, 1839

Diagnosis. Usually selectively preserved, winding to regularly meandering, more or less horizontal trails, consisting of a central back-filled tunnel enveloped by an even to lobate zone of reworked sediment. Commonly, only the external part of the enveloping zone is preserved as a densely packed uni- or multi-serial chain of small depressions or pustules (From Uchman 1995).

Remarks. The taxonomic distinction between *Nereites* MacLeay, *Neonereites* Seilacher, and *Scalarituba* Weller has been a contentious issue (*cf.* Chamberlain 1971; Fillion & Pickerill 1990; Uchman 1995). The differing morphological expressions represented by these three taxa are considered by some authors to represent behavioural variations of the trace maker and thus should be maintained as separate ichnotaxa (Seilacher & Meischner 1965; Seilacher 1983, 1986). Well preserved transitional specimens suggest that these three ichnogenera actually represent preservational variants of the same basic morphology and as such require synonymization (Chamberlain 1971; Uchman 1995, 1999). Based on material lacking the transitional forms, some authors maintain a distinction between *Nereites* and *Neonereites* (e.g. Hakes 1976; Pickerill 1980, 1981; Crimes, *et al.* 1981; Fillion & Pickerill 1990). The lack of transitional forms does not exclude the method of preservation from being the primary cause of morphological

variation and is unacceptable for use as an ichnogeneric delimiter regardless of the prominence of the taxa being synonymised (Uchman 1995).

The primary diagnostic characteristic of *Nereites* burrows is considered to be the central core surrounded by variably preserved marginal lobes (Uchman 1999). The key morphology of *Nereites* burrows is considered to reflect the feeding pattern of the trace maker as it deposit feeds from the sediment surrounding the burrow, defecating behind itself as it moves through the sediment (Callow *et al.* 2013a). *Nereites* is the eponymous taxon of the archetypal *Nereites* ichnofacies which has traditionally been considered to be restricted to deep marine environments (Seilacher 1967). In more recent studies, however, it has been documented in shallow marine settings, particularly in the Palaeozoic (Mángano *et al.* 2000; MacEachern *et al.* 2007; Uchman & Wetzel 2011; Callow *et al.* 2013b).

Nereites irregularis (Schafhäutl, 1851): Uchman, 1995 Fig. 7A

Diagnosis. Relatively small *Nereites* with usually closely packed, gregariously occurring deep meanders, which exhibit a tendency of coiling. Meanders, usually of variable dimension and regularity, in adjacent levels or even at the same level. The envelope zone usually thinner than the central tunnel; in closely packed meanders it touches or overlaps with neighbouring segments, in more loose meanders it displays low lobes. Commonly the envelope zone is not preserved. A back-fill structure is poorly manifested (from Uchman 1995).

Description. Tightly winding burrows *c*. 3-5 mm thick preserved in sandstone. Meanders typically form *c.* 3 cm organised bundles preserved in convex hyporelief. Marginal lobes of *c*. 2 mm thickness are poorly preserved.

Remarks. Nereites irregularis was originally described as *Helminthoida irregularis* Schafhäutl but was later transferred to *Neonereites irregularis* (*cf.* Seilacher 1967; Chamberlain 1971). Upon synonymization of the ichnogenus *Neonereites* with *Nereites,* the taxon became *Nereites irregularis* (Uchman 1995).

Nereites missouriensis Weller, 1899 Fig. 7B

Diagnosis. Variably preserved, loosely meandering to winding *Nereites* with wide, central back-filled tunnel and envelope zone of similar thickness, which occasionally displays low side lobes. The exterior may be expressed as uni- or multi-serial chain of closely packed sediment pustules. The interior may be preserved as a row of at least uni-serial closely packed sediment depressions, or as strongly flattened burrows, which form usually colour-contrasted strips on parting surfaces with poorly preserved or not-preserved side lobes (from Uchman 1995).

Description. Predominantly horizontal winding burrow composed of dark, clay rich central core of *c*. 2-5 mm thickness, surrounded by a zone of clean sandstone *c*. 1-3 mm thick. Mostly occurring within clay rich heterolithic strata.

Remarks. Following the documentation of well-preserved transitional forms of *Scalarituba* to *Neonereites*, *Neonereites uniserialis* was moved to the older *Scalarituba missouriensis* which had priority (Chamberlain 1971; Chamberlain & Clark 1973). The ichnogenus *Scalarituba* was later shown to display all the diagnostic features of *Nereites* and was deemed a subjective synonym by Uchman (1995).

Nereites missouriensis is often preserved in four distinct varieties: 1) faecal ribbon form; 2) thin-meniscate form; 3) thick-meniscate form; and 4) lobate form (cf. Uchman 1995). Of these only the faecal ribbon form has been recorded from the Stainmore Formation near Howick.

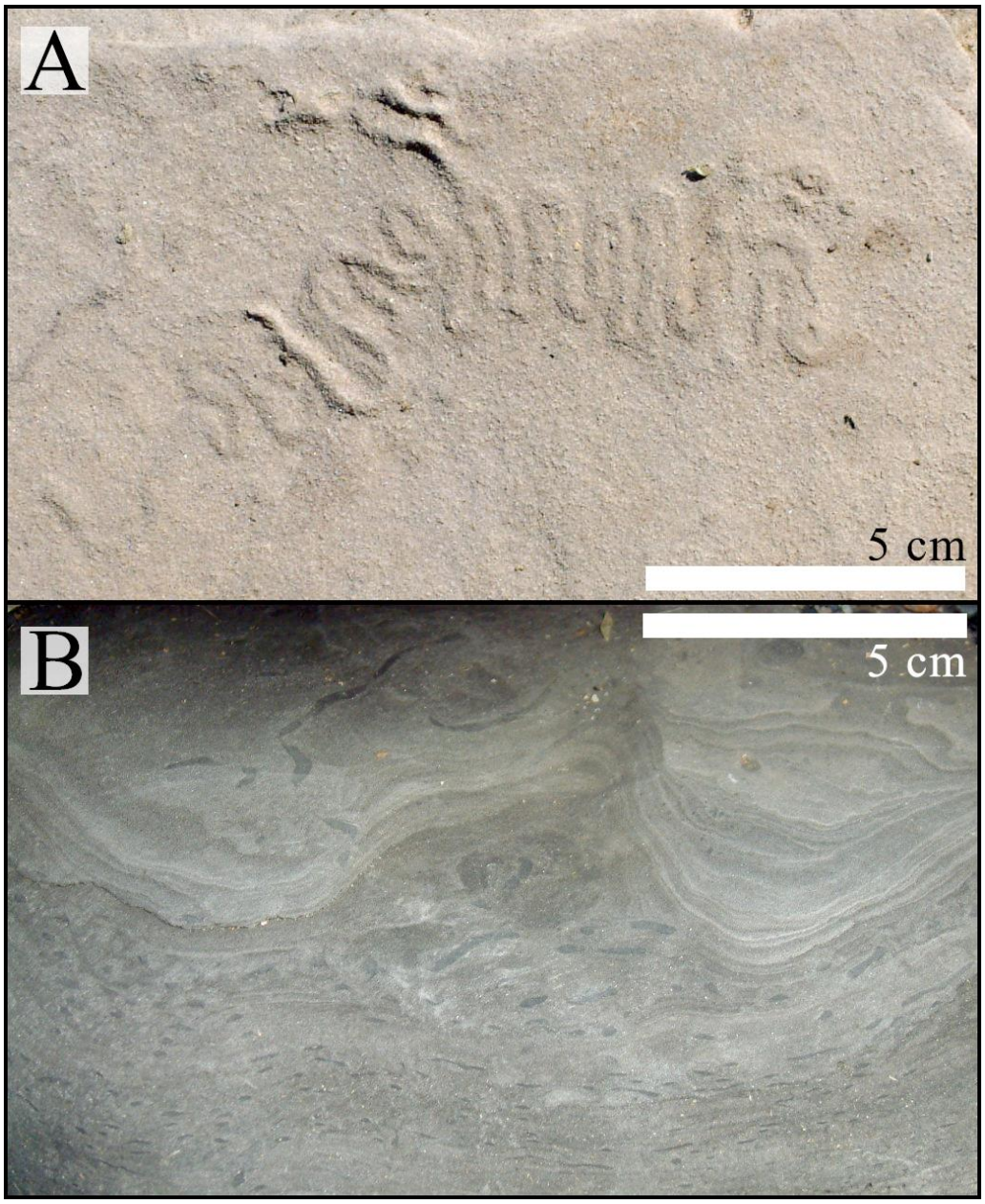

Figure 7. A) *Nereites irregularis* B) *Nereites missouriensis* - faecal ribbon form (*sensu* Uchman 1995).

Ichnogenus **PSAMMICHNITES** Torell, 1870

Type Ichnospecies. Psammichnites gigas (Torell 1868): Fischer & Paulus, 1969

Diagnosis. Predominantly horizontal, sinuous, meandering to looping traces with transverse or arcuate internal structure and a distinct median dorsal structure, commonly represented by a sinusoidal or straight ridge/groove, or regularly spaced circular mounds/ holes. Preserved in full relief on top of beds or, more rarely, in negative hyporelief (From Mángano & Rindsberg 2003).

Remarks. Psammichnites is a broad ichnogenus with the potential for numerous taphonomic variants (*cf.* Mángano & Rindsberg 2003). The key unifying feature is considered to be the median dorsal structure (Mángano & Rindsberg 2003). The trace maker remains unknown but candidates range from gastropods (Fenton & Fenton 1937a) to an organism related to halkieriids (Seilacher-Drexler & Seilacher 1999).

In a recent extensive study of *Psammichnites* several ichnogenera (*Plagiogmus* Roedel 1929, *Olivellites* Fenton & Fenton 1937b, *Aulichnites* Fenton & Fenton 1937b) were considered to be morphological or taphonomic variants, and synonymized with *Psammichnites* (Mángano & Rindsberg 2003). Of those synonymized, *Plagiogmus* is the most problematic.

Although superficially similar, *Plagiogmus* is composed of multiple components, some of which are not found in *Psammichnites* (cf. McIlroy & Heys 1997). Notably, we do not consider the basal “ladder” component of *Plagiogmus* to be purely a taphonomic

expression, but rather constructed as the result of locomotory process of the trace maker (cf. McIlroy & Heys 1997). Although *Plagiogmus* has distinct and differentiating components from other ichnospecies of *Psammichnites*, the ichnotaxononomic weight of these components requires further assessment of type material. Given the variations presently accounted for within various specimens of *Psammichnites*, *Plagiogmus arcuatus* may be considered as belonging within *Psammichnites,* but as a distinct ichnospecies.

Psammichnites plummeri (Fenton & Fenton, 1937b): Chamberlain 1971 Fig. 8

Diagnosis. Psammichnites with relatively straight dorsal continuous ridge or groove and fine, closely spaced, transverse ridges (From Mángano & Rindsberg 2003).

Description. Back-filled winding trace with pronounced dorsal structure, typically a ridge. Burrow width ranges from 6-20 mm with upper lengths in excess of one meter. Arcuate back-filled sediment is arranged in finely space even packets of *c*. 1 mm. Burrow path ranges from straight to highly sinuous and does not branch or self-cross (Figure 8A). Burrows occasionally coincide with conical collapse structures (Figure 8B-C). Burrows are commonly found throughout the succession, in silt rich and heterolithic units.

Remarks. Psammichnites plummeri burrows from the Howick succession were first described by Tate (1859) as fossilized examples of annelids. A new genus was created to accommodate two species present at the Howick succession, *Crassopodia*

embletonia and *Crassopodia media* (Tate 1859). *Crassopodia media* was subsequently deemed a *nomen dubium*, whereas *C. embletonia*, a *nomen oblitum*, is considered a junior synonym of *Psammichnites plummeri* (Mángano & Rindsberg 2003). Although the name *Psammichnites embletonia* has priority over *P. plummeri, P. plummeri* is widely used in the literature and in the interest of nomenclatural stability it is retained (Mángano & Rindsberg 2003).

Psammichnites plummeri is considered to be the result of both feeding and locomotory processes (Yochelson & Fedonkin 1993; Mángano & Rindsberg 2003). The feeding strategy of the trace maker likely involved deposit feeding on the sediment in front of and around itself; it likely also fed on sediment transported downward through collapsing sediment around itself (Figure 8 B-C).

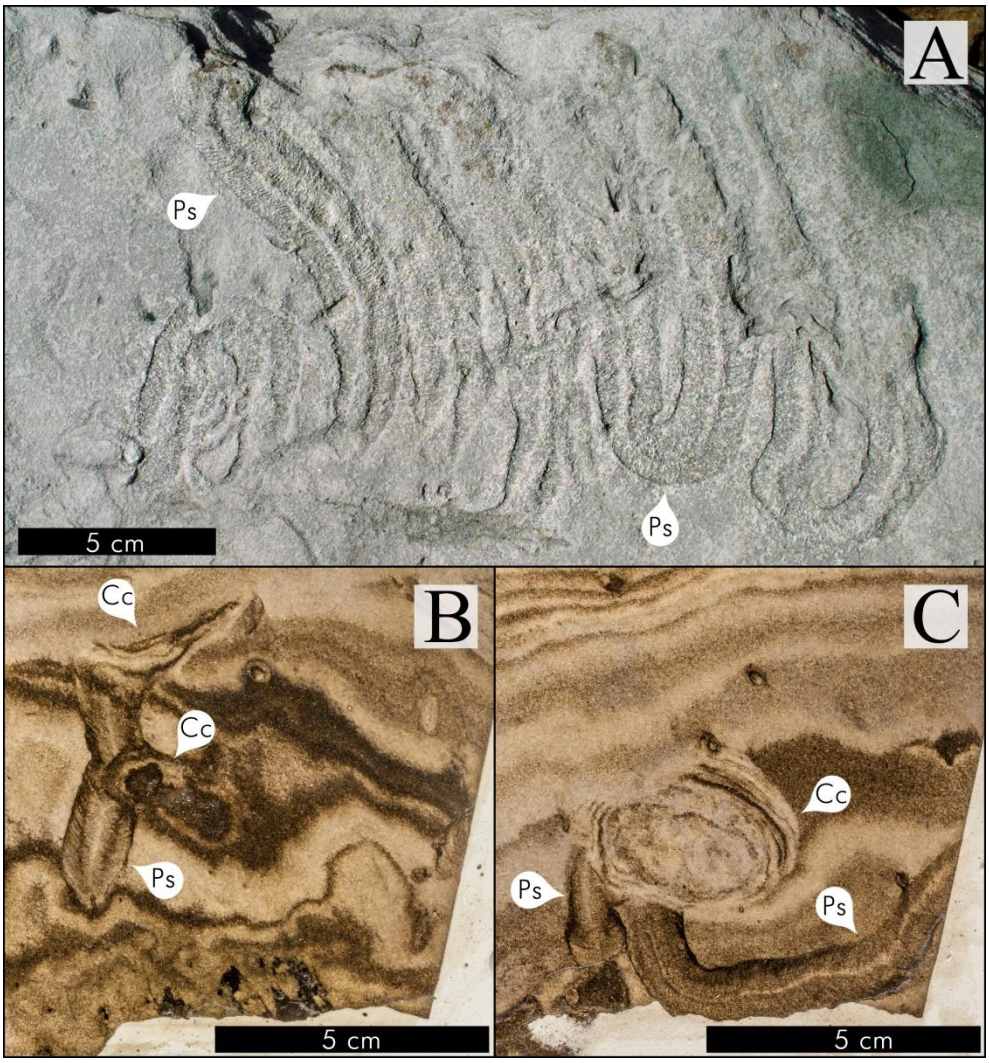

Figure 8. *Psammichnites plummeri* (Ps) A. Field photograph showing sinuous winding pattern. B-C. Grind images separated by 2.1 mm demonstrating interaction between two *Psammichnites plummeri* burrows and conical collapse structures (Cc).

Ichnogenus **RHIZOCORALLIUM** Zenker, 1836

Type Ichnospecies. Rhizocorallium jenense Zenker, 1836

Diagnosis. Horizontal to oblique, U-shaped spreite burrow (From Knaust 2013).

Remarks. Rhizocorallium is a well-documented and easily recognized trace fossil that has experienced a lot of taxonomic discussion, with over 20 ichnospecies having been included within the ichnogenus (*cf.* Fürsich 1974; Knaust 2007; Schlirf 2011; Knaust *et al.* 2012; Knaust 2013). *Rhizocorallium* has undergone significant revision and consolidation through the revision and synonymization done by Fürsich (1974) whereby only three ichnospecies were considered valid: 1) *R. jenense* Zenker, 1836, 2) *R. irregulare* Mayer, 1954, and 3) *R. uliarense* Firtion, 1958. This classification has subsequently been determined to be an oversimplification following examination by topotype material (Knaust 2007, Knaust *et al.* 2012, Knaust 2013). Although the number of valid ichnospecies was reduced to just *R. jenense* and *R. commune* Schmid, 1876, these ichnospecies have been further broken down into ichnosubspecies and varieties (Knaust 2013). This classification facilitates the ability for individual workers to quickly identify ichnotaxa at the ichnospecies level, but allows for detailed study to further classify the trace should they chose.

Rhizocorallium jenense, previously synonymised by Fürsich (1974) is considered a senior synonym of *R. irregulare* by Knaust (2013), and is used to describe steeply

inclined, passively filled, firmground *Rhizocorallium*. Primarily horizontal with pronounced spreite, typically in softground, *Rhizocorallium* are attributed to *R. commune*.

Rhizocorallium commune Schmid, 1876 Fig. 9

Diagnosis. Rarely branched burrows with a preferred sub-horizontal orientation. The burrows are elongate, band-like, straight or winding, and may have sub-parallel longitudinal scratches on the wall. Faecal pellets (*Coprulus* isp.) are common within the actively filled spreite and the marginal tube (After Knaust 2013).

Description. U-shaped, predominantly horizontal, spreiten burrows grouped into two forms. 1) Stubby (*c*. 10 cm long by *c*. 2.5 cm wide) burrows with faintly preserved spreite and relatively thick marginal tubes (*c*. 1 cm; Figure 9A). 2) Long and winding burrows in excess of 30 cm with well-preserved clay rich spreite. Burrow width is *c*. 7cm with a marginal tube of *c*. 1.5cm (Figure 9B).

Remarks. Rhizocorallium commune is further classified into two ichnological sub-species and two varieties. *Rhizocorallium commune problematica* describes burrows with vertically retrusive spreite, while *R. commune uliarense* characterizes burrows with an overall spiral morphology (cf. Knaust 2013). *Rhizocorallium commune* can also be described using two ichnovarieties, *irregulare* (for long and winding burrows) and *auriforme* (for stubbier, slightly inclined burrows; cf. Knaust). Both varieties of

Rhizocorallium commune are preserved in the heterolithic beds of the Stainmore Formation near Howick. This designation is made using overall morphology and using the burrow-size ratios described by Knaust (2013).

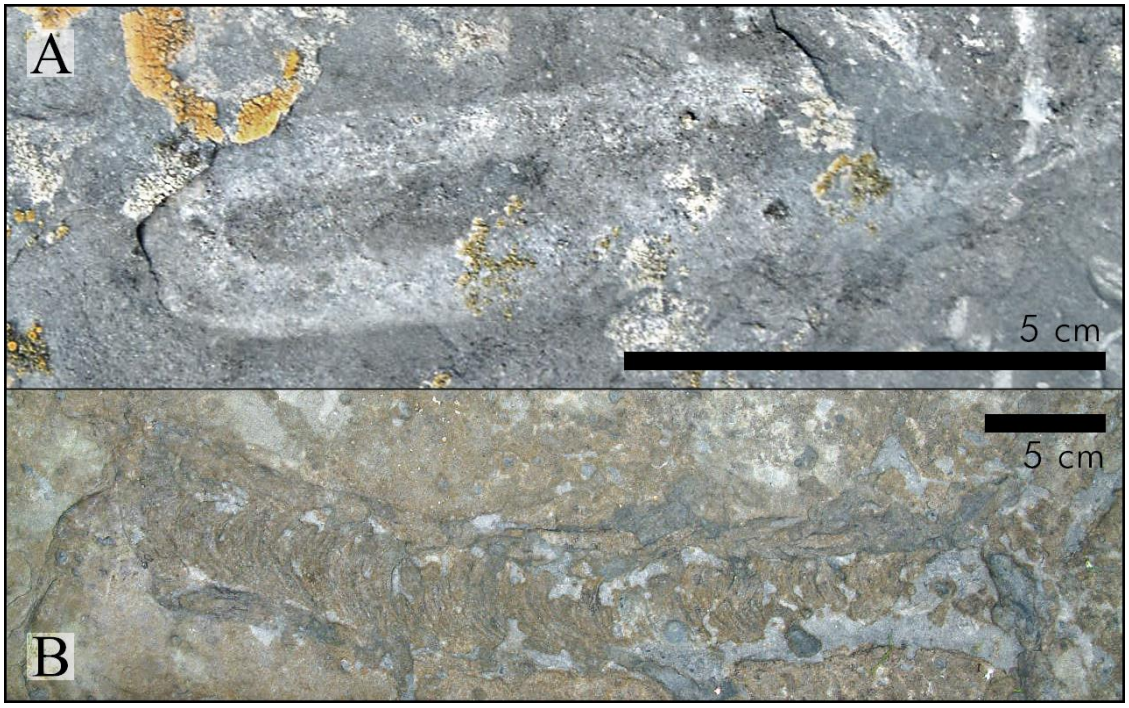

Figure 9. *Rhizocorallium commune* A) *R. commune* var. *auriforme* B) *R. commune* var. *irregulare*

Ichnogenus **TEICHICHNUS** Seilacher, 1955

Type Ichnospecies. Teichichnus rectus Seilacher, 1955; by monotypy

Diagnosis. Elongate spreiten structure consisting of primarily horizontal stacked gutter-shaped laminae (after Fillion & Pickerill 1990).

Remarks. Teichichnus is considered to have been formed by vertically adjusting the position of a burrow component of consistent shape through the surrounding sediment (Mørk & Bromley 2008). Proposed reasons for this adjustment include maintaining a consistent depth beneath the sediment water interface and bringing fresh sediment into the burrow cavity (*cf.* Seilacher 1955; Frey & Bromley 1985; Mørk, & Bromley 2008).

Teichichnus stellatus Baldwin, 1977 Fig. 10

Diagnosis. Curved, cylindrical, retrusive, spreite-filled tubes radiating from a single central point to form a more or less symmetrical stellate pattern (After Baldwin 1977).

Description. Cylindrical tubes of consistent diameter (5-6 mm) bearing retrusive spreite radially arranged around a central point. Clearly visible tubes display micaceous linings within a sandstone matrix. Although the central shaft has not been observed associated with this material, one is inferred. The possibility remains that the radiating tubes are simply straight tubes which pass through a common point.

Remarks. Teichichnus stellatus is rare in the literature. This may be the result of apprehension in the designation of material to the ichnospecies given its similarities to other ichnogenera (*cf.* Seilacher 2007). *Teichichnus stellatus* bears strong comparisons with *Dactyloidites canyonensis* as described by Fürsich and Bromley (1985), however this material has subsequently been demonstrated to be based on pseudofossil material

(Cloud 1960; Runnegar & Fedonkin 1992). The distinction of *T. stellatus* from *Dactyloidites* requires further study including the examination of the type material of *D. asteroides.*

Figure 10. *Teichichnus stellatus* with eight distinct limbs, and three partly preserved limbs, that may radiate from a central point.

CONCLUSIONS

This study provides a systematic re-assessment of the ichnological assemblage of the Stainmore Formation near Howick, Northumberland. The fossil assemblage of the Howick succession was originally described by Tate in 1859, and it was one of the first descriptions of an ichnological assemblage (Tate, 1859). In his original descriptions Tate

(1859) introduced the new genera *Eione* and *Crossopodia*, which have subsequently been transferred to *Neoeione* (Boyd and McIlroy, in review) and *Psammichnites* (Mángano & Rindsberg 2003) respectively.

Lithologically, the Stainmore formation is composed of repetitive cycles of mudstones, siltstones, sandstones, as well as thin limestones and coals (Dean *et al.*, 2007). It is considered to represent recurring cycles between marine and deltaic environments (Dean *et al.*, 2007). The succession near Howick, studied herein, is composed of interbedded thick, storm reworked, sandstone, siltstone, and mudstone. These upward coarsening deposits are considered to represent a prograding, storm-dominated, shoreface deposit within a marine cycle of the Stainmore Formation.

Ten ichnotaxa belonging to nine ichnogenera are documented herein, and are inferred to represent diverse and varied trace maker ethologies. The assemblage includes burrows inferred to represent dwellings, as well as a range of feeding strategies including grazing, deposit feeding, and potential farming. The storm dominated sandstones exhibit a high ichnodiversity and lower overall bioturbation as compared with the mudstone units.

The palaeoecological and palaeoenvironmental information reflected in the ichnological assemblage aid in the understanding of the local ecosystem and palaeoenvironmental conditions at the time of deposition. Despite intermittent periods of high energy events, the local ecosystem continually responded creating a range in traces likely reflecting a stable and biodiverse community of organisms.

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CHAPTER SIX

THREE DIMENSIONAL TOMOGRAPHIC RECONSTRUCTION OF AN EXCEPTIONALLY WELL PRESERVED ICHNOLOGICAL ASSEMBLAGE FROM THE STAINMORE FORMATION, CARBONIFEROUS, UK: **PROJECT SUMMARY AND CONCLUSIONS.**

1. Summary

Trace fossils are named and classified according to the ICZN (1999) in a manner comparable to biotaxa. Although trace fossils are the fossilized works of organisms, biotaxa and ichnotaxa cannot be directly compared. Zoological taxonomy categorizes taxa within hierarchical groups using evolutionary descendancy and close common ancestry. As many different organisms can produce the same traces and a single organism can produce many different traces, trace fossils cannot be linked to specific trace makers with certainty, and as such evolutionary schematics cannot be practically applied to ichnotaxa. Many trace fossils have been classified purely on the basis of the inferred trace making organism, or the trace maker ethology, however this is subjective by nature and should be avoided (Goldring *et al.*, 1997). Trace fossil descriptions and classification should be based primarily on morphological assessment (Bromley, 1990, 1996; Pickerill 1994; Bertling *et al.*, 2006; Bertling, 2007). In an effort to maximize the practical applications of ichnology, many authors suggest basing the significance, in terms of use

as an ichnotaxobase, of morphological components on the inferred ethology (Bromley, 1990, 1996; Pickerill 1994; Bertling *et al.*, 2006; Bertling, 2007; Knaust, 2012).

A thorough understanding of trace fossil morphology is essential in properly classifying and defining ichnotaxa. A key component of understanding trace fossil morphology is to create an understanding of the inherent range of morphologies that are present when defining new ichnospecies. Many ichnospecies have undergone significant revision and require synonymization owing to taphonomic, preservational, and slight ethological variations being introduced as distinct taxa (*e.g. Nereites* [Uchman, 1995]; *Psammichnites* [Mángano and Rindsberg, 2003]). Initial assessment of the inherent morphological and taphonomic variants, as well as the utilization of a type series (as opposed to a single holotype) could substantially aid ichnotaxonomists and reduce the confusion surrounding an ichnotaxon, particularly in the case of traces resulting from highly facultative organisms.

1.1 Review of objectives

A thorough understanding of a given trace fossil is difficult to establish prior to a complete three-dimensional characterization using techniques comparable to serial grinding and morphological modelling (*cf.* Bednarz and McIlroy, 2009; 2012; Boyd *et al.*, 2012; Bednarz *et al.*, 2015; Leaman *et al.*, 2015). This study used a combination of established and novel analytical techniques to thoroughly characterize the ichnological assemblage present in the Stainmore Formation near Howick, United Kingdom. Three prevalent ichnotaxa in need of careful examination where chosen for dedicated study using the serial grinding and morphological modelling techniques described by Bednarz

et al. (2015; Appendix A): 1) *Dactyloidites jordii* isp. nov.; 2) *Beaconites capronus*; 3) *Neoeione moniliformis* igen. nov. comb. nov. This location was chosen for the excellent preservation of various trace fossils within high contrast heterolithic sediment that accentuates otherwise subtle morphological components of the ichnotaxa.

1.2 Review of the methodology

This study utilized a combination of analytical approaches, including established and novel techniques. The field locality for this study was the Bashkirian aged Stainmore Formation from the coastal cliffs near Howick, in the United Kingdom (55°27’30.38”N, 1° 35’34.32”W). Approximately 4.5 m of the heterolithic inter-bedded sandstone and siltstone/mudstone succession was logged using conventional and digital methods. Samples were collected from closely localized float and transported to Memorial University of Newfoundland for analysis. The mineralogical composition was assessed using X-ray diffraction. Several samples were sub-sampled and used to create both blue dye impregnated and non-dyed petrographic thin sections. The blue dye impregnated thin sections were serially photographed at 200X magnification and digitally processed automatically to assess the porosity distribution across the slides (Appendix B). Several samples were encased in plaster and serially ground and photographed according to the methodology described by Bednarz *et al.* (2015; Appendix A). Several improvements were made to this process throughout the study:

1) Enhancements to the lighting and consistency during the photography of the samples allowed for true, full colour modelling of the burrow systems.

Full colour modelling of the burrow systems allows for easy visual assessment of any lithological differences throughout the sample (*e.g.*, sandstone versus mudstone).

2) Alterations in the modelling techniques allowed for three-dimensional modelling of the entire rock sample prior to modelling the extracted burrow selections.

Modelling the whole rock sample prior to modelling the isolated burrow systems allowed early insight into the complex three dimensional burrow morphology, aiding in the digital burrow selection process. Additionally, modelling the whole rock sample allowed for easy visualization of any sedimentary structures within the sample (*e.g.*, conical collapse structures, sediment laminations, etc.) that would otherwise be challenging to extract. The whole rock model proved very beneficial when assessing the relationship between the burrow system and the surrounding sediment.

3) Improved rendering efficiencies and more powerful computers allowed multiple burrows, burrow components, and the whole rock sample to be modelled simultaneously.

Visualizing multiple burrow systems within a single model allowed for assessment of the interrelationship of the different burrows or burrow components within the sample. This also allowed burrow-rich areas of the sample to be viewed as a whole, with the option to quickly isolate portions of the system to assess in greater detail.

1.3 Outcomes of CHAPTER TWO

A review of the ichnogenus *Dactyloidites* was undertaken, and the new ichnospecies *D. jordii* was introduced. The excellent preservation of material from the

field locality allowed for highly detailed three dimensional modelling of a radiating burrow system that was hitherto undescribed. Using petrographic techniques, x-ray diffraction, and three dimensional modelling this burrow system was thoroughly assessed. The complex radiating morphology of *D. jordii* isp. nov. was described and used to make inferences regarding the ethology and palaeobiology of the trace maker.

The probable trace maker is herein considered to be a vermiform organism that formed the radiating burrow system by repeated probing outward in search of food. The organism is demonstrated to have an adaptive nature, resulting in variable burrow morphology. The facultative nature of the trace maker is demonstrated by a change in burrowing pattern at an erosive surface in the sample, indicating that the organism shifted burrowing behaviour upon encountering non-ideal sediment; a sandstone layer with low clay content. The variable burrow morphology resulting from facultative trace maker behaviour highlights the need for ichnologists to introduce new ichnotaxa using a type series as opposed to a single type specimen.

Three specimens of *D. jordii* are named as syntype material for this study and are housed at The Rooms (the provincial museum of Newfoundland and Labrador) in the natural history collection. One specimen is preserved in convex epirelief and mostly still encased in sediment. The radiating probes of a second specimen were thin section transversely and longitudinally and these thin sections stand as type slides. The final syntype specimen was serially ground and photographed producing a high-resolution three dimensional model; the original serial photographs are being housed as digi-syntype material (*sensu* Adams *et al.*, 2010).

1.4 Outcomes of CHAPTER THREE

Beaconites capronus is a common trace throughout the succession. Chapter three fully characterized and described this ichnotaxon using both field observations and high-resolution models. The detailed burrow morphology facilitated inferences on palaeobiology and ethology of the trace maker. Several different burrows were selected and modelled to fully characterize the burrow morphology. The horizontal winding portion of *B. capronus* as well as directly connected vertical pipes were modelled. The vertical portions of *B. capronus* are identical in morphology to the horizontal sections, and are actively back-filled with the same diagnostic chevron shaped meniscate. The vertical pipes were actively back-filled as the organism descended into the sediment, illustrating the need for a mechanism of coping with the resultant low-oxygen pore water. This issue is handled in various methods by organisms including: 1) revisiting the sediment-water interface; 2) creating periodic shafts (e.g., Bromley and Asgaard, 1975; Plaziat and Mahmoudi, 1988); or 3) employing the use of obligate anaerobic metabolism (cf. Danovaro et al., 2010; Mentel and Martin, 2010). Currently there is no way of differentiating which method or combination thereof the organism may have used, and this area of study requires further investigation.

Although the *Beaconites capronus* burrows from the Howick succession tend not to self-cross, regular secondary successive branching is demonstrated herein. As the trace making organism would defecate into the burrow, this labile material may have facilitated the growth of microbial matter thus encouraging re-bioturbation in the form of coprophagy.

1.5 Outcomes of CHAPTER FOUR

A taxonomic review of the burrow system originally introduced as *Eione moniliformis* Tate was undertaken. *Eione* Tate was created in 1859 for what was considered to be a new genus of annelid (Tate, 1859). However, prior to this the name *Eione* had been previously introduced for a genus of gastropod thus making *Eione* Tate a junior homonym of *Eione* Rafinesque (Rindsberg, 1994; Buckman, 2001). *Eione* Tate was subsequently transferred to *Parataenidium* Buckman to stabilize the ichnotaxon (Buckman, 2001).

Parataenidium was created for predominantly horizontal burrows distinctly composed of two levels (Buckman, 2001). The type ichnospecies, *P. mullaghmorensis*, clearly shows multiple levels within the burrow, with the upper level inferred to be a faecal component and the lower level inferred to be the result of locomotion (Buckman, 2001).

Using serial grinding and high-resolution modelling the detailed morphology of *Parataenidium moniliformis* is assessed herein. The resultant models clearly demonstrate that *P. moniliformis* is composed of a single back-filled level. *Parataenidium moniliformis* is demonstrated to be composed of serial inclined sediment packages of reniform shape that are closely packed and cross-cut one another, giving an imbricated appearance. Transverse cross sections of the burrow near the joining of two sediment packages can give the illusion that the burrow is composed of two distinct levels. As *P. moniliformis* does not match the ichnogeneric diagnosis of *Parataenidium*, the transfer of *Eione moniliformis* to *Parataenidium* is herein rejected and the new ichnogenus *Neoeione* is created to accommodate *Eione* Tate.

Given the recognition of dramatically different burrow morphology, a new palaeobiological model is proposed for *Neoeione moniliformis* igen nov. comb. nov.

1.6 Outcomes of CHAPTER FIVE

A systematic assessment of the ichnological assemblage of the Stainmore Formation from the coastal outcrop near Howick, Northumberland was completed. Ten ichnotaxa, belonging to nine ichnogenera, have been described reflecting a diverse and well preserved assemblage. The ichnotaxa described reflect various ethologies including locomotory processes, dwellings, and numerous feeding strategies including grazing, deposit feeding, and potential farming traces. The information reflected by the ichnological assemblage aid in the understanding of the local palaeoecological and palaeoenvironmental conditions at the time of deposition. The local ecosystem produced a range in traces likely reflecting a stable and biodiverse community of organisms despite intermittent periods of high energy events.

2. Concluding statement

Applied ichnology is a combination of both sedimentology and palaeontology that is of highly useful to both fields of study (McIlroy, 2008). Ichnology continues to develop and is being used more frequently in palaeoenvironmental studies, reservoir characterization, biostratigraphy, and sequence stratigraphy (*cf.* MacEachern *et al.*, 1990; Taylor and Gawthorpe, 1992; Taylor and Goldring, 1993; Gingras *et al.*, 1999, 2004;

Savrda *et al.*, 2001; Taylor *et al*., 2003; MacEachern and Burton, 2005; Pemberton and Gingras, 2005; McIlroy, 2008; Bednarz and McIlroy, 2009). The usefulness of ichnology depends on proper morphological description and accurate understanding of the ichnotaxa involved. Three dimensional morphological reconstructions are essential to fully characterizing and understanding these structures (*cf.*, Bednarz and McIlroy, 2009; 2012; Boyd *et al.*, 2012; Bednarz *et al.*, 2015; Leaman *et al.*, 2015). This thesis highlights the need for a thorough understanding of the three dimensional morphology of a trace fossil when proposing new ichnotaxa or considering the palaeobiology/ethology of trace makers.

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APPENDIX A

Automated precision serial grinding and volumetric 3D reconstruction of large ichnological specimens

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Abstract

We present herein a methodology for obtaining deterministic three-dimensional reconstructions of large or complex trace fossils and volumetric approach to the reconstructed models. Two stages are outlined: a laboratory stage, involving precision serial grinding and high-resolution digital photography, and a computer analysis stage, where burrow volumes are visualized and analysed. It is shown that the techniques can be used successfully for bioturbated rocks that have little or no density contrast between the matrix and the burrows, upon which non-destructive techniques, such as CT scanning, are ineffective. The serial grinding method employing automated, computer-controlled machinery, enables precise removal of extremely thin, parallel increments of sedimentary rock. After each grinding run, a high-resolution digital photograph of the specimen surface is taken. From this, computer analysis of the generated stack of images allows high-resolution, 3-D reconstruction of the trace fossils, and subsequent visualization of burrow morphology, volume, and sedimentological impact. To demonstrate the technique, several trace fossil samples (phycosiphoniform burrows, *Chondrites*, *Ophiomorpha*) were serially ground and digitally photographed. We show that the method enables volume calculations to be determined precisely for a single burrow, burrow networks and ichnofabrics.

INTRODUCTION

Serial grinding has been used to reconstruct the three-dimensional morphology of paleontological specimens for over a century (*e.g.*, Sollas, 1903; Stensio, 1927; Ager, 1965; Tipper, 1976; Herbert and Jones, 2001; Watters and Grotzinger, 2001). With the advent of low-cost digital photography and fast, high-quality image-processing software, the approach has become increasingly accessible, and the techniques developed by Sutton *et al.* (2001a, b, 2005, 2006) for studying the body fossils of the Herefordshire Lagerstatte have proved particularly influential. With the high-resolution, easily manipulate-able images produced, and the wealth of morphological data that can be garnered, this approach has now been applied to a variety of fossil material (*e.g.*, Rahman and Zamora, 2009; Maloof *et al.*, 2010).

Despite its potential value in elucidating morphology and sedimentological impact, serial grinding and computer modelled 3-D reconstruction has been little used in ichnology. Exceptions are the trace fossil studies of Naruse and Nifuku (2008), Bednarz and McIlroy (2009, 2012), Michalik and Šimo (2010), and Boyd *et al.* (2012). Other studies have used serial polishing to examine ichnofabrics and trace fossils, but without the creation of 3-D computer modelled volumetric reconstructions.

Serial grinding and 3-D reconstruction of trace fossils and ichnofabrics in large rock samples have never been attempted, but such work is critical to full morphological characterization of many ichnotaxa (*cf.*, McIlroy *et al.*, 2009). Since trace fossils can comprise volumetrically significant components of many sedimentary rocks – affecting

sedimentological properties at a reservoir scale (Buatois *et al.*, 2002; Gingras *et al.*, 2004; Burns *et al.*, 2005; Gordon *et al.*, 2010; Tonkin *et al.*, 2010; Bednarz and McIlroy, 2012), it is vital to understand their three-dimensional morphology.

Volumetric 3-D reconstruction of such trace fossils has the potential to provide new insights into reservoir characterization. Several techniques have been used previously to obtain spatial models of the burrowing activity of living animals, or to measure the volumes of trace fossils and ichnofabrics. These include computed axial tomographic (CT) scanning (*e.g.*, Dufour *et al.*, 2005; Herringshaw *et al.*, 2010), magnetic resonance imaging (MRI) (*e.g.*, Gingras *et al.*, 2002), multi-stripe laser triangulation scanning (MLT) (Platt *et al.*, 2010) and serial grinding (Naruse and Nifuku, 2008; Bednarz and McIlroy, 2009, 2012; Michalik and Šimo, 2010; Boyd *et al.*, 2012). All these methods have their limitations, depending upon the examined rock or sediment properties.

The density contrast between matrix and burrow is commonly low, and it can be difficult to determine the true morphology of a trace fossil from two-dimensional cross-sections. As such, only destructive serial grinding can be employed satisfactorily to obtain a volumetric 3-D reconstruction of a burrow (*cf.*, Gingras *et al.*, 2002; Naruse and Nifuku, 2008; Bednarz and McIlroy, 2012). In most paleontological and ichnological studies, the serial grinding has been carried out manually (*e.g.*, Wetzel and Uchman, 1998; Sutton *et al.*, 2001a; Bednarz and McIlroy, 2009). While this is acceptable for small specimens, such an approach is not appropriate for larger ones, as it is too unwieldy and imprecise.

By using serial grinding to produce high-resolution reconstructions, new information can also be obtained on the ecology of the trace-maker and the sedimentological impact of bioturbation. Furthermore, such studies can be used to resolve ichnotaxonomic issues by resolving trace fossil morphology within the host sediment. This approach to ichnological and ichnotaxonomic research is particularly relevant if applied to specimens from the type locality (Boyd *et al.*, 2012).

The aim of this paper is to present a method used to model trace fossils in three dimensions, and to apply deterministic volumetric approach that is beneficial in ichnotaxonomy and also in bioturbated reservoir studies.

METHODOLOGY

SAMPLE PREPARATION

Large blocks containing multiple or single trace fossils of various size can be trimmed in the field using a hand-held rock saw, if care is taken to leave sufficient matrix around the trace fossil. In our study, to create a regular shape for precise image alignment, each block was placed in a box and plaster of Paris poured around it (*cf.*, Bednarz and McIlroy, 2009, 2012; Boyd *et al.*, 2012). Once the plaster is set, the block is removed from the box, and cut into a rectangular prism using a laboratory rock saw. The regular outline of the block is used as the basis for image registration (*see* below; Fig. 1A). For further accuracy of image alignment, vertical holes can be drilled into the block (*cf.*, Sutton *et al.*, 2001a). Prior to photography (*see* below), visual contrast between the

ichnofabric and the rock matrix can be enhanced considerably by wetting the ground surface of the specimen with water or a light oil (*cf.*, Bromley, 1981). To prevent disintegration of the plaster of Paris from frequent moistening, non fossil-bearing surfaces of the block can be coated with plain, transparent lacquer.

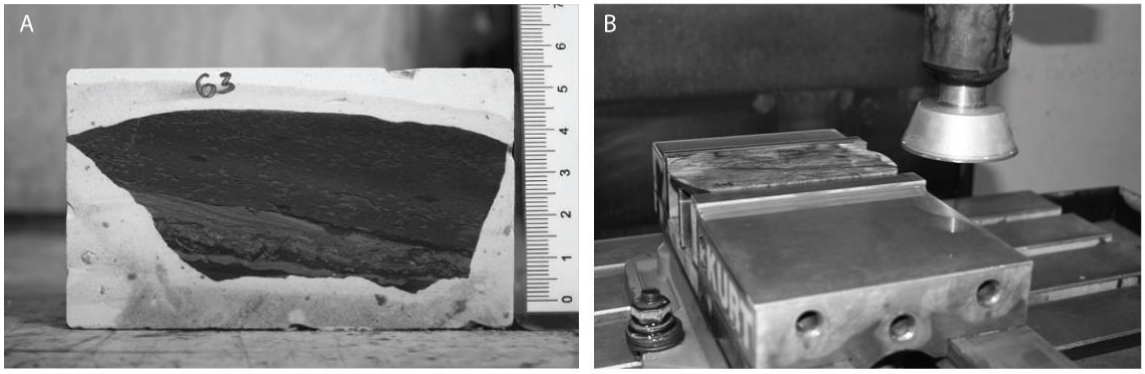

Figure 1. *Set-up and procedure for precise, computer-controlled serial grinding of ichnological samples.* **A)** *Freshly exposed surface of sample embedded in plaster of Paris, ready for photography;* **B)** *HAAS VF-3 CNC Vertical Machining Center, showing diamond-tipped rotating blade with sample clamped in place prior to grinding.*

SERIAL GRINDING SET-UP

Serial grinding was carried out using a Haas VF3 VOPC Vertical Machining Center (20hp vector dual drive, 1000 IPM), capable of grinding to a precision of 0.001 inch (0.025 mm). Specimens were clamped in place (Fig. 1B), using the gantry, raised by remote control to the start position, and then raised by the required increment after each grinding run. The most effective grinding element was found to be a diamond disc (diameter = 70 mm).

The increment of rock removed during each serial grinding run can be varied according to the dimensions and expected complexity of the material studied. For example, phycosiphoniform burrows with a diameter of 2–3 mm were serially ground at increments of 0.2 mm; whereas a block containing *Diplocraterion* with a width of ~60 mm and an estimated depth of over 100 mm, was serially ground at increments of 0.4 mm. The choice of serial grinding interval resolution depends also on the purpose of the reconstruction, with coarser increments used for gross-scale reconstructions, and finer increments used to provide highly detailed reconstructions and to enable volume measurements of small specimens.

PHOTOGRAPHY

Canon 30D and 50D digital SLR cameras were used to photograph the specimens after each grinding run. For accuracy in the subsequent registration process (*see* below), it is crucial to maintain the distance between the freshly exposed sample surface being photographed, and the objective (lens) of the camera being used. Owing to the fact that the sample decreases in thickness after each run of the grinding tool, the camera–specimen surface distance was adjusted each time to ensure consistency.

The photographs should be taken under invariant lighting conditions that best illuminate the ichnofabrics. To test this, a series of photographs of the same sample surface should be taken under different conditions, after the first serial grinding run. Lighting conditions to consider include photography under ambient lighting, under flash lighting, and under controlled directional lighting. It is essential to avoid shadows across

the sample, which might obscure important features or be confused subsequently as being of lithological origin.

If contrast is insufficient when the rock surface is dry, it may be necessary to wet the surface to enhance the contrast: this is particularly true of finer grained rocks, or specimens where the trace fossil fill is of a similar colour to the matrix. Images from successively ground surfaces should be consecutively numbered using a permanent marker or pencil, and photographed with a scale bar (Fig. 1A).

DIGITAL IMAGE-PROCESSING AND INTERPRETATION

Images can be processed using a range of filters (*e.g.*, brightness, contrast) in a 2-D graphic software package such as Adobe Photoshop to enhance the contrast between the burrow and the matrix. Depending on the characteristics of the sample, the photographs may need to be changed to greyscale to do this effectively.

In the worked examples considered here, each photograph of the serially ground sample was stacked consecutively as layers in a single Photoshop file (.PSD). The first photograph in the series was used as a base layer, and all other layers were registered (aligned) with this base layer. Each successive layer was named using the number of the serial grinding run captured in the photograph.

BURROW SELECTION METHODS

Once all images are aligned, the image stack was cropped to focus on the area of interest. The burrows are selected, either by mouse or tablet pen, using one of the many

tools in Photoshop (*e.g.*, "Magic Wand" or "Pen"). The choice of tool depends upon the nature of the burrows (Fig. 2A and D). If the burrows are large and the contrast between them and the matrix is sufficient, the "Magic Wand" tool can be used. If the burrows are small, however, and the contrast between the trace fossil and matrix minimal, the "Magic Wand" tool might select a range of pixels that do not belong to the burrow, introducing errors (*cf.*, Fig. 2B and E) and overly complex 3-D isosurfaces (*see* below). The most accurate – but time-consuming – method of burrow selection is to use the 'Brush' and 'Magnetic Lasso' tools with a tablet pen (Fig. 2C and F). These tools enable the most accurate selection of burrow shape and minimize production of spurious burrow margins.

When the examined ichnotaxon is known to be composed of more than one element (*e.g.*, *Nereites*, Fig. 2A–C; *cf.*, Bednarz and McIlroy, 2009, 2012), all elements can be selected separately. This makes it possible to reconstruct different elements of the same burrow separately in 3-D. In addition, modelling different components of the burrow separately in the same 3-D volume enables artificial colouring of the different components of the trace fossil, and can be used for volume measurements of these separated elements and their comparisons. The burrow selection layers are then saved as grey-scaled images, with white silhouettes on a black background.

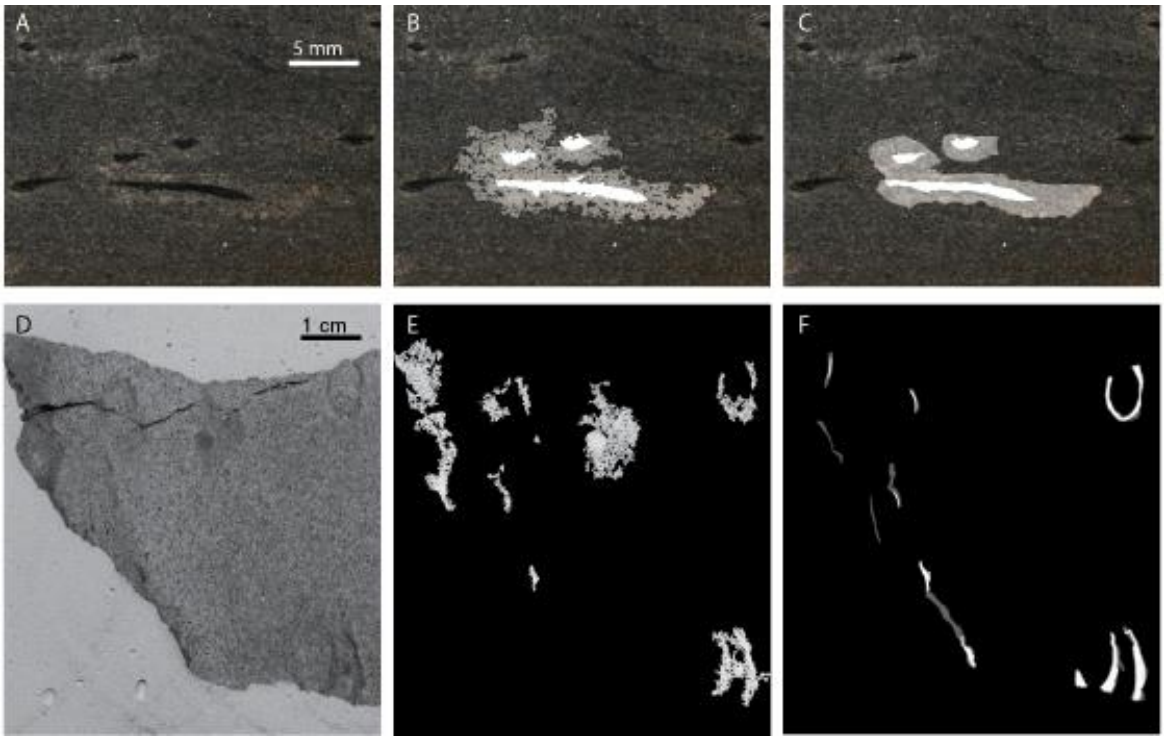

Figure 2. *Selection of features in two samples of serially ground trace fossil: phycosiphoniform burrows* (**A, B, C***; composed of two elements: core and halo) and* Ophiomorpha *burrows* (**D, E, F**)*. Phycosiphoniform burrow core shown in white in images* **B** *and* **C***; burrow halo in grey.* **A, D)** *Images showing polished surface of ichnological samples, prior to burrow selection.* **A)** *Black shapes represent burrow cores surrounded by haloes of lighter coloured material in low contrast to matrix material;* **D)** *Dark grey areas represent muddy lining/fill of* Ophiomorpha *burrows;* **B, E)** *Shapes of burrows obtained using Magic Wand selection tool. Pixelization of burrows visible, resulting from imprecise nature of the tool.*

3D MODELLING

In this study, stacks of the images that are to be reconstructed were imported into the commercial edition of one of two 3-D volume visualization software packages: VG Studio Max 1.2, and VolView 2.0. Both programs can reconstruct spatial geometry from

a sequence of 2-D images representing the cross-sections of any object or structure, by the process of voxel (volume element) rendering. When importing raster image formats such as .JPG or .PNG into the programs sample spacing values (x, y and z) must be provided manually.

1. Volume Visualization and Polygonal Surface Extraction

The burrow volumes are visualized as 3-D objects by the software on the basis of the greyscale iso-values of the voxels in merged 2-D slices. Volume generation is calculated by the connection of voxels with the same grey intensity in each consecutive image (iso-grey-value surface; Fig. 3B). Thus obtained, the 3-D volumes of the trace fossils can be artificially coloured to better visualize different elements of the trace fossil (*e.g.*, Fig. 3A and C).

Volumetric studies of trace fossils and ichnofabrics require that the external morphology of the reconstructed burrows be 'polygonized'. The polygonal models of reconstructed burrows are generated from the volumetric datasets through isosurface extraction (Fig. 4A). Polygonal surface extraction is based on the grey-scale or opacity iso-value that is chosen to be the most accurate representation of the object being reconstructed (Fig. 4B). The polygonal mesh created is exported at 1:1 scale into the .SLT file format (Stereo Lithography 3-D object) that can be opened and edited by most 3-D modelling programs (*e.g.*, Autodesk 3ds MAX).

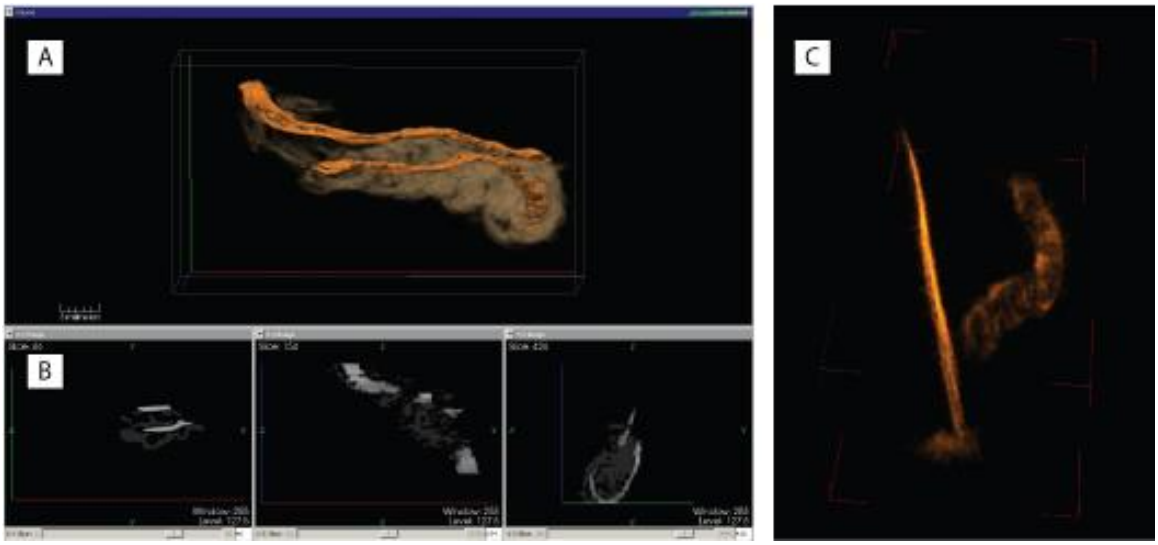

Figure 3. *Application of artificial colours for visual enhancement of burrow structures.* **A)** *Reconstruction of* Phycosiphon*-like burrow in 3-D: core shown in orange; halo in grey.* **B)** *Series of 2-D slices (planes: x-y, x-z and y-z) showing phycosiphoniform burrow elements (core and halo) in greys of dual intensity (iso-grey-values); screenshot of reconstructed specimens from Rosario Formation, Mexico, generated in VolView software;* **C)** *Reconstruction of* Ophiomorpha *from Blackhawk Formation, Utah; screenshot generated in VG Studio.*

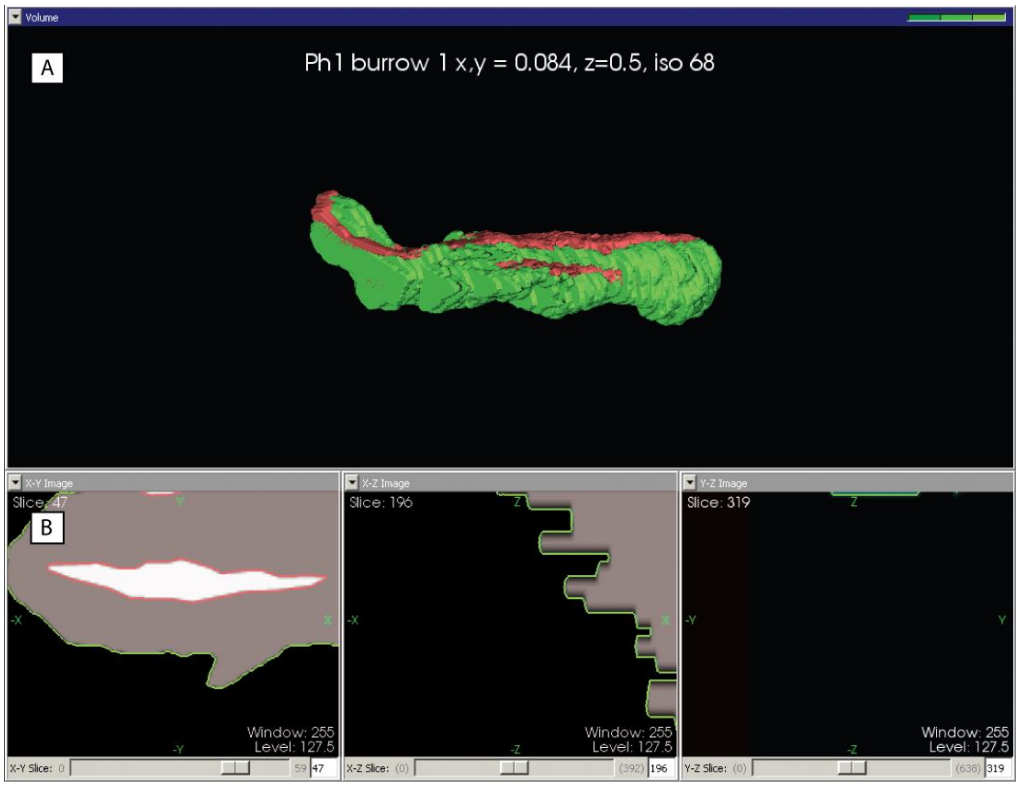

Figure 4. *Polygonal surface extraction of reconstructed* Phycosiphon*-like burrow from Rosario Formation, Mexico, based on iso-grey-values; screenshots generated in VolView software.* **A)** *Resultant polygonal surface showing core (red) and halo (green);* **B)** *Surface component lines applied to iso-grey-values of distinct burrow elements (core and halo) in each of 2-D slices (planes: x-y and x-z).*

2. 3-D Modelling Software and Polygonal Mesh Optimization

The mesh of the generated polygonized objects reflects the three-dimensional morphology of the modelled trace fossil. The mesh originally generated by the software is dense, composed of millions of triangle-shaped polygons, and usually contains duplicated vertices and faces as well as isolated fragments and open holes. As a result, the file containing the mesh is usually very large and needs considerable system and graphic card memory to be opened and edited. Therefore it must be optimized, simplified and/or re-

meshed to reduce the number of polygons (decimation) (Fig. 5). The surface of the polygonized trace fossil must also be smoothed to account for the unknown distribution of the trace fossil surface between the known two dimensional planes (the two images representing the two surfaces of the rock exposed during two consecutive serial grinding runs), which have been averaged in the process of creating voxels.

In this study, the first stage of simplification was achieved in the volume-visualizing software prior to exporting the mesh. Further simplification and optimization can be accomplished using most 3-D modelling programs (*e.g.*, MeshLab v1.2.2 or Autodesk 3ds MAX). The resultant 3-D objects were further modified by: 1) the application of artificial colours to the specified volumes of distinct transparency (representing different density or porosity within the specimen); 2) the cropping of reconstructed volumes along specified planes; 3) the isolation of discrete burrows as detached objects; and 4) the rotation and animation of objects. Volumetric binary data obtained through digital reconstruction can be exported to many file types that maintain the 3-D structure. This enables further examination using freeware software, such as Right Hemisphere Deep View, GLC_Player, and Cortona3D Viewer. Exporting burrow reconstructions to widely used, interactive file formats allows for further investigation of 3-D morphology by the creation of artificial cross-sections, animations, visualization of connected high porosity zones in three dimensions, and the measurement of volumes of the different burrow components (*cf.*, Bednarz and McIlroy, 2012).

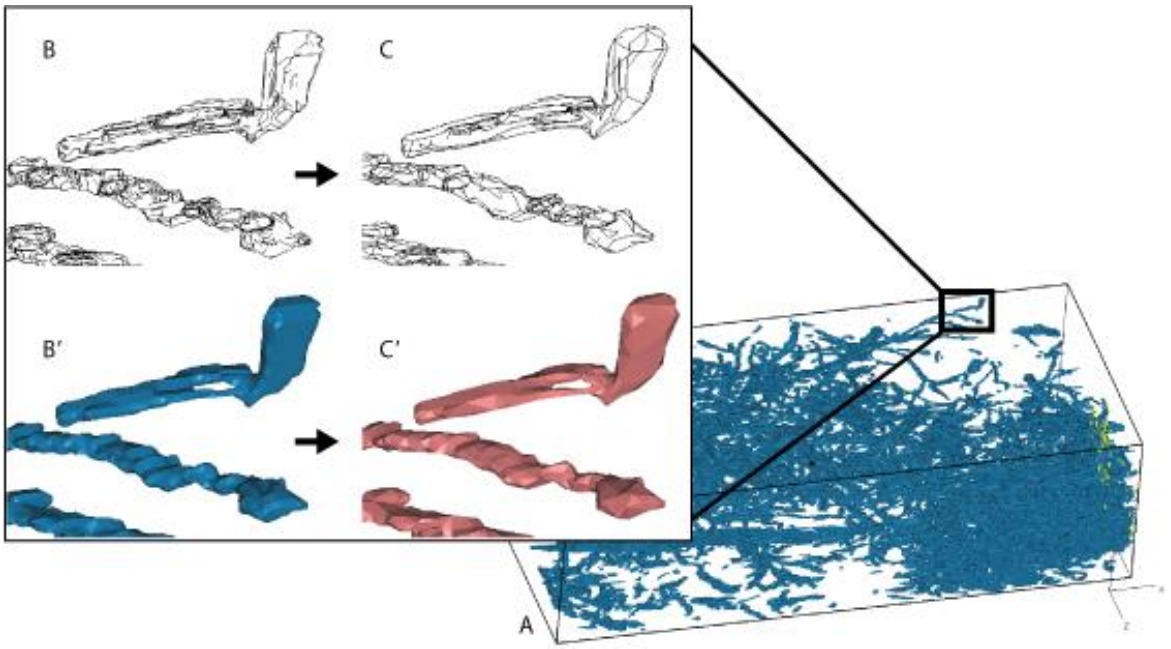

Figure 5. *Mesh simplification of reconstructed trace fossils.* **A)** *Polygonized 3-D model of* Chondrites *Ichnofabric. Mesh was exported as .STL file from VolView software and was 314 MB in non-simplified mesh format.* **B, B')** *Zoomed-in selection of non-simplified polygonized mesh;* **C, C')** *Zoomed-in selection of simplified polygonized mesh (decimated, optimized, smoothed). Resultant simplified mesh file size reduced to 68 MB.*

VOLUMETRICS IN ICHNOLOGY

Once a polygonized surface is created, it is possible to apply a volumetric approach to the three-dimensional models characterizing the reconstructed burrow or ichnofabric. The volume or surface area of the polygonized ichnological model can be measured directly by VolView, or by using a third-party program such as Autodesk 3ds Max.

Recent studies have revived volumetric approaches in ichnology (*see* Platt *et al.*, 2010; Bednarz and McIlroy, 2012). Distances and angles can be measured in any 3-D modelling or volume-visualizing software. From a volumetric perspective, the most valuable measurements are those of surface area and volumes of the examined burrow or ichnofabric, which are either given in metric units or as relative magnitudes in percentages.

Surface area (SA, after Platt *et al.*, 2010) is a measurement of the polygonal surface area generated by the volume-visualizing software. It is crucial to measure the optimized polygonal mesh to avoid flawed results, such as those caused by overlapping polygons (Platt *et al.*, 2010).

There are two main volumes that describe any burrow or ichnofabric. These are: 1) the volume of a prism bounding the ichnofabric or the whole preserved burrow or partly preserved burrow, or *volume available* (VA, *after* Platt *et al.*, 2010); and 2) the volume of the burrow or ichnofabric itself, or *volume utilized* (VU, *after* Platt *et al.*, 2010). VA is the volume of the smallest rectangular prism (width = a, height = b and length = c) that encloses the burrow, preserved part of the burrow or burrow association (Fig. 6):

$$(1)\ VA = a \cdot b \cdot c$$

The volume of the entire burrow or burrow association is the VU, calculated using the 3-D software, and describes the amount of the sediment reworked by the tracemaker.

On the basis of these volumes, further measurements can be made. These describe and quantify the characteristics of the measured burrow or ichnofabric in relation to the main volumes (VA and VU), as follows:

Volume exploited (VE) describes burrow density and the efficiency of space usage by the tracemaker, reflecting the percentage of the volume of the sediment that was reworked by the tracemaker. It is calculated using the following equation (*after* Platt *et al.*, 2010):

$$(2)\ VE = {}^{VU \cdot 100}\!/_{VA}$$

Volume component percentage (%Vcomp) represents the volumetric contribution of a particular component (Vcomp) of the burrow or ichnofabric, when reconstructed separately (*e.g.*, the core or halo of *Phycosiphon*). %Vcomp is calculated as a percentage of the VA:

$$(3)\ \%Vcomp = {}^{Vcomp100}\!/_{VA}$$

If the length of some component of the burrow (L) is known (by measurement using the 3-D modelling software), the tortuosity index (T) can be calculated.

The tortuosity index is the ratio between the diagonal length (d) of a rectangular prism bounding the burrow, and the total length of the burrow (L):

$$(4)\ T = {}^{d}\!/_{L}$$

When calculated for a burrow that does not branch or intersect itself at any point (*i.e.*, a string, as observed in ichnotaxa such as *Phycosiphon*, *Helminthoida*, *Nereites* and *Spirorhaphe*), the T value can illustrate the degree of burrow sinuosity and how densely it

is packed in three dimensions (through consideration of value of d within the equation; Equation 4). In cases when the burrow is branched or intersects itself, the T value indicates how densely the burrow is packed within the burrow-bounding 3-D prism, but not necessarily its curvature (*e.g.*, *Chondrites*, *Thalassinoides*, *Ophiomorpha*). T values vary between 0 and 1, with straight burrows having a T value equal one or close to one (*e.g.*, T=0.9 for an individual Nereites burrow; Fig. 6D), and highly tortuous/densely packed burrows having a T value that approaches zero (*e.g.*, T=0.3 for a highly tortuous burrow in Fig. 6C).

Measurements of lengths and angles can be made in the 3-D modelling software while examining the polygonal mesh of the models. A variety of possible measurements can be applied to different trace fossils, such as examining the branching angles of *Chondrites*, or the inclination of a burrow relative to the bedding.

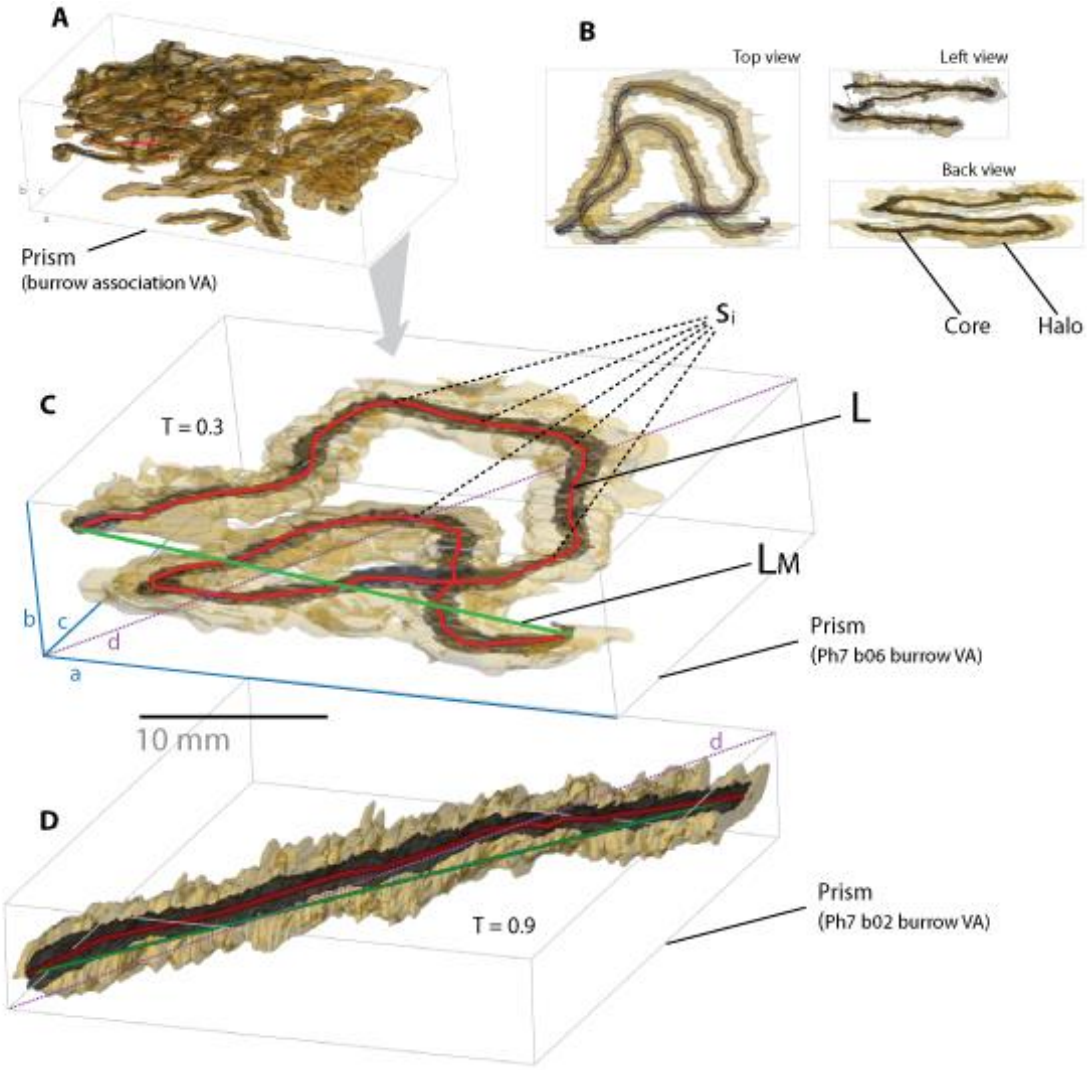

Figure 6. *3-D model of reconstructed ichnofabric composed of* Nereites *burrows (Lower Carboniferous Yoredale Sandstone Formation, Northumberland, U.K.).* **A)** *Reconstruction of burrow network;* **B)** *Individual burrow (Ph7 b06) isolated from reconstructed burrow network, shown in top, lateral, and back views;* **C)** *Reconstruction of burrow Ph7 b06, showing tortuosity value (T) = 0.3;* **D)** *Reconstruction of burrow Ph7 b02 from same sample network, showing tortuosity value (T) = 0.9. Symbols: VA – Volume Available; Si – straight elements composing core length line; L – core length; LM – marginal length; T – Tortuosity index; a, b, c – prism dimensions; d –diagonal space within prism.*

POPULARIZATION OF 3-D INTERACTIVE MODELS

To enable the most comprehensive use and investigation of 3-D ichnological models, it is beneficial to generate file formats that can display any polygonal mesh in an interactive 3-D environment, and which can be opened with a dedicated 3-D viewer installed on the user's computer system (*see* Table 1 for popular 3-D software). The best formats for this are .PDF with 3-D models embedded, .STL, .OBJ and .WRL files. WRL and PDF files also offer the possibility of publishing the interactive reconstructions on the internet, and are therefore the most desirable file formats in terms of rapid sharing and dissemination of 3-D models and data (*see* example of interactive 3-D model embedded in the PDF file in Appendix 1). All the file formats listed above can be generated in most forms of 3-D modelling software, such as Autodesk 3ds Max.

Table 1. List of 3-D software used for visualizing, modeling and viewing 3-D models

Software	Type	Website	License
VGStudio Max	3D volume visualizing (reconstruction)	www.volumegraphics.com	commercial
VolView	3D volume visualizing (reconstruction)	www.kitware.com	commercial
Autodesk 3ds Max	3D modeling software	www.autodesk.com	commercial
MeshLab	3D modeling software	meshlab.sourceforge.net	freeware
DeepView	3D viewer	www.righthemisphere.com	freeware
GLC_Player	3D viewer	www.glc-player.net	freeware
Cortona3D Viewer	3D viewer	www.cortona3d.com	freeware
Adobe Acrobat Reader	3D viewer	http://www.adobe.com	freeware

APPLICATIONS AND FUTURE WORK

Three-dimensional reconstructions of trace fossils and ichnofabrics give ichnologists the possibility to review or determine the true morphology and geometry of any ichnological specimen. Deterministic calculations of the true volumes and surface areas of trace fossils also provide new insights of significance to reservoir studies (Bednarz and McIlroy, 2012). When evaluating ichnological impact on reservoir quality, the volumetric assessment of the trace fossils or ichnofabrics is probably the most significant factor. Depending on the characteristics of the reconstructed trace fossils, their volumetric description can help determine reservoir quality. *Phycosiphon*-like burrows, for example, can significantly increase the reservoir quality of mudstones in unconventional shale-gas plays as their silt-rich burrow haloes can create porous and permeable zones within otherwise impermeable host rocks (Bednarz and McIlroy, 2012). Three-dimensional visualization of such biogenic pore networks is thus highly relevant to hydrocarbon reservoir characterization. Future work on 3-D reconstructions is likely to enhance the availability/accessibility of 3-D models and streamline their generation to make them a widely used tool for ichnologists and petroleum geologists.

Three-dimensional reconstructions of trace fossils and other ichnologically generated sedimentary fabrics have the potential to greatly inform ichnotaxonomic studies, as well as paleobiological and paleoecological models accounting for the processes of burrow formation and modification. At present, with few exceptions (*Macaronichnus*: Gingras *et al.*, 2002; phycosiphoniforms: Naruse and Nifuku, 2008;

Bednarz and McIlroy, 2009, 2012; *Zavitokichnus*: Michalik and Šimo, 2010; *Ophiomorpha*: Boyd *et al.*, 2012), the true and deterministic morphology of many common, ichnofabric-forming trace fossils is not known. It has been shown recently that there are at least three trace fossils that produce similar 'frogspawn' ichnofabrics in vertical cross-section, while having considerably different three-dimensional geometries (Bednarz and McIlroy, 2009, 2012).

The method described herein may have limitations when applied to totally bioturbated sediments, especially if employed for ichnotaxonomic studies. High bioturbation index and/or presence of burrows that intersect each other may considerably reduce the lucidity of the component single burrows and thus influence the resultant reconstruction of the burrows' spatial morphology.

However, in terms of resolution, the presented method employing high-res photography and a chosen computer controlled serial grinding machinery can be used to make extremely precise reconstructions because the diamond-coated grinding tip can remove a rock layer as thin as 1 micron (*cf.*, Maloof *et al.*, 2010). Although time consuming, manual selection of the ichnofossil's shape components gives the confidence that the obtained spatial structure is not flawed by the elements, that could be erroneously interpreted as a burrow's elements by the automatic selection tools which usage may result in incorrect spatial structure and further volumetric measurements.

CONCLUSION

Automated, computer-controlled, serial grinding allows for very precise abrasive removal of extremely thin, parallel portions of examined rock samples (up to 1 micron). This method creates the possibility of obtaining – through digital photography – a large number of high-resolution images showing the three-dimensional structure of ichnological specimens. The reconstruction process necessitates the careful, and time-consuming, manual selection of burrows within these photographic images using 2-D software. This precision, however, plays a vital role in the subsequent reconstruction of the trace fossils with volume-visualizing software. After the volume has been reconstructed, it is possible to produce a polygonal mesh of the trace fossil surface that can be the basis for volumetric analysis. Quantification of many burrow or ichnofabric parameters can then be calculated once the polygonal mesh is produced, including: 1) burrow dimensions; 2) the volume of sediment that the tracemaker reworked; 3) the surface area of the burrow; and 4) burrow tortuosity.

When the 3-D models are exported to popular file formats, they can be made widely accessible to researchers, giving the opportunity for further analytical work. This volumetric approach to ichnology is likely to have a particularly significant impact in petroleum geology, where the characterization of trace fossils has already proven to have a major effect on the permeability and fracturability characteristics of reservoir intervals (Buatois *et al.*, 2002; Gingras *et al.*, 2004; Burns *et al.*, 2005; Gordon *et al.*, 2010; Tonkin *et al.*, 2010; Bednarz and McIlroy, 2012)

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APPENDIX B

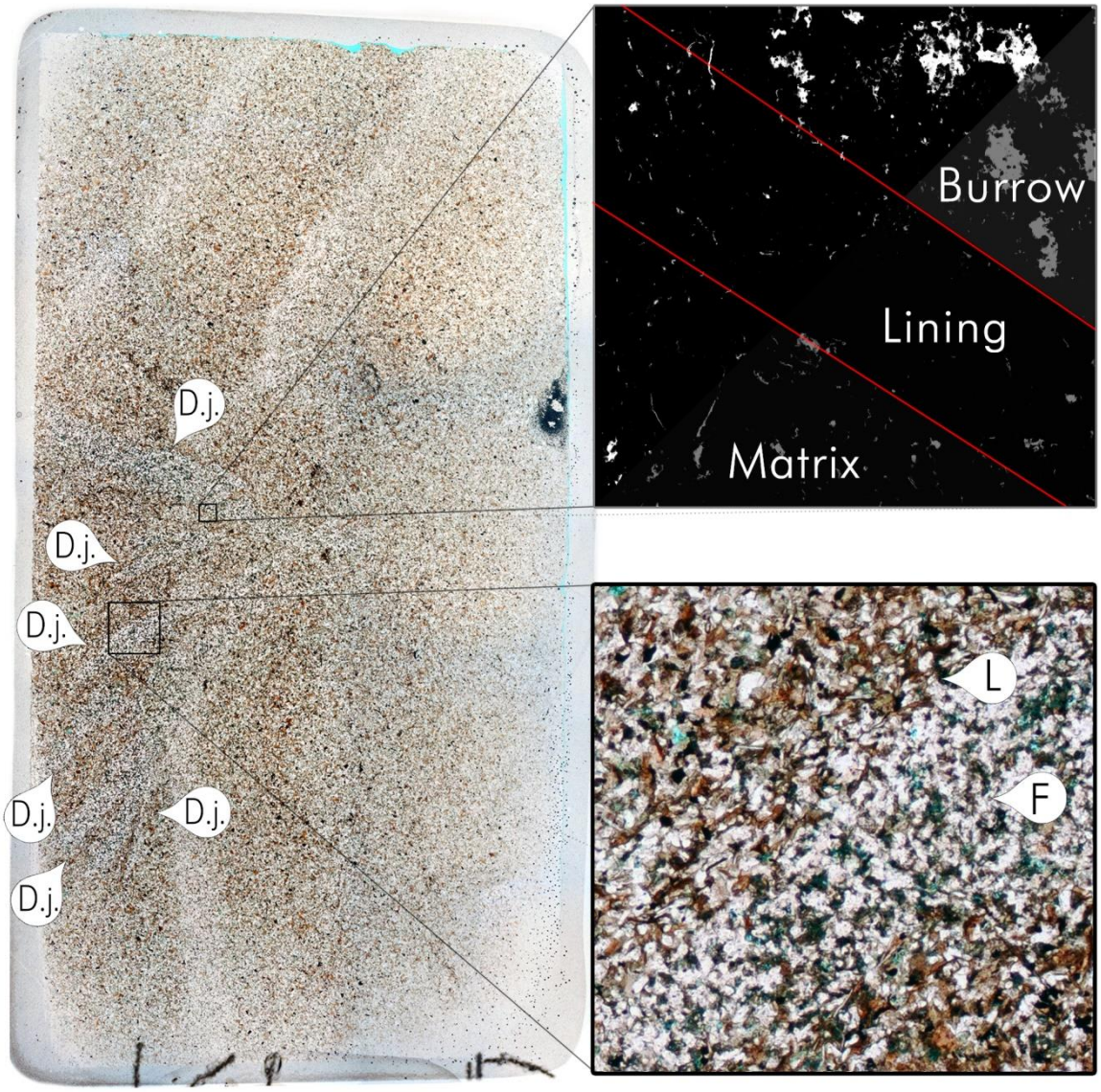
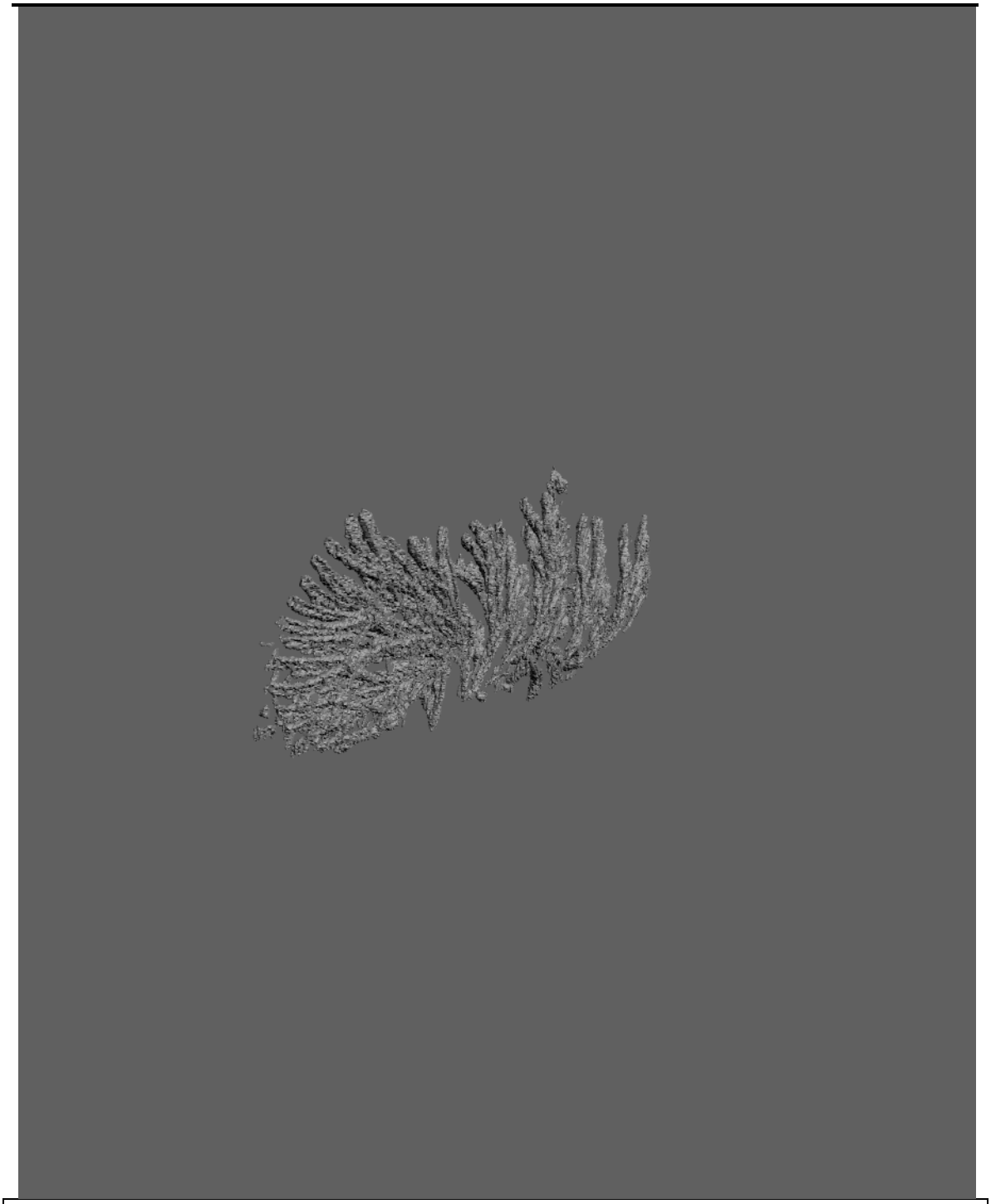


Image composite from 1400 photomicrographs showing the longitudinal cross section of radiating *Dactyloidites jordii* tubes. The slide was blue-dye impregnated to fill the open pore space. The blue dye was then digitally extracted to calculate porosity percentages. L indicates the burrow lining, F indicates the burrow fill. Porosity measurements for the burrow fill are typically c. 6%, the matrix porosity is c. 2-3%. The porosity of the burrow lining is typically less than 1%

APPENDIX C



Interactive model of *Dactyloidites jordii* isp. nov. produced using serial grinding and photography modelling techniques.

APPENDIX D

Three dimensional colour animation of *Dactyloidites jordii* isp. nov.